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PHYLOGENETIC SIGNIFICANCE OF THE PORES IN UREDIOSPORES [1]

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A prominent feature of the urediospores of most species of the Uredinales is the presence of visibly differentiated areas in the walls of the spores through which germination takes place. The Tulasnes (**35**) first observed and illustrated these morphologic features in 1847 and applied the name of pores or oscules to them. Their taxonomic value in the rusts of grasses and sedges was pointed out by Arthur and Fromme (**5**) in 1915, and the possible importance of their arrangement was suggested by Fromme (**19**) in 1915 and again by Buller (**10**) in 1924. A comparative study of the pores of any number of genera or of a large number of species within a single genus has not previously been made.

While such a detailed study has not been made, the systematic value of the number and arrangement of the pores in urediospores

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has been attested by their almost universal inclusion in specific descriptions. The present clarity of specific limits in the rusts of grasses and sedges is, in large measure, the result of careful study of the pores in the urediospores. Aside from experiments establishing the alternate hosts no single feature has proved as helpful. Although granting the advance facilitated by the use of this character no data have been presented to validate such usage from other than a purely descriptive basis. The pores in the teliospores have often been employed in the interrelation of genera, those in the urediospores only rarely. It is possible, however, to accord phylogenetic importance to the number and arrangement of the pores in urediospores, as will be shown.

Both the number and the arrangement of the pores in the urediospores vary according to the species studied. The pores may be scattered, bizonate, equatorial, superequatorial, subequatorial or limited to a ring about the hilum. The number is also variable, ranging from a single pore to as many as twenty. The pores may be large and evident or small and obscure. A small, hyaline, cuticular cap is often present over the pore but may be wanting. Sculpturing on the wall of the spore may cover the area above the pore or an otherwise sculptured wall may be smooth around the pore. In the midst of this variability it is striking that this morphologic feature remains constant, with rare exceptions, for any given species. Such constancy, aside from being convenient for the systematist, may be indicative of phylogenetic value and if so should offer a means of reaching a better understanding of the interrelationships of the genera and species.

An attempt is made in the following pages to evaluate this morphologic feature and to explain the phylogenetic significance of the different numbers and arrangements of pores.

In order to reach the conclusions presented, it has been necessary to start from some basic assumption regarding the phylogeny of the rusts. The view that the rusts of the family Melampsoraceae are more primitive than those of the family Pucciniaceae has been accepted and the conclusions reached will be seen to require the acceptance of such a view as essentially valid.

The data presented in this paper were obtained chiefly from a

study of the rust flora of North America as presented by Arthur (2) in the North American Flora.

THE UREDIOSPORE-PORES OF THE MELAMPSORACEAE

The urediospores of 84 species in 14 genera of the Melampsoraceae of North America were examined. Visible pores were found to be characteristic of the spores of all of the genera, although they could not be definitely demonstrated in some species.

In preparing the urediospores for study they were mounted in a saturated solution of chloral hydrate and heated to the boiling point. At times it was necessary to repeat the heating. By boiling in this manner the outer, sculptured, cuticular layer can often be dissolved, as in *Chrysomyxa*. The pores are then visible in the inner wall of the urediospore. Spores devoid of their protoplasm offer the most favorable material for examination. Gentle pressure upon the cover slip will usually crack the wall of the spores sufficiently to liberate the contents. The above methods of treatment are helpful but main reliance must be placed upon a careful manipulation of the microscope, and the eye must be trained to see indistinct differences in the structure of the walls.

With the exception of verrucose urediospores, such as characterize *Coleosporium* and *Chrysomyxa*, the pore is usually covered by a small, hyaline, cuticular cap which protrudes beyond the uniform curvature of the wall and into which the pore does not extend. This cap or umbo may be similarly sculptured as the rest of the cuticular layer or it may be smooth. The cuticular caps expand in water and a careful search for them often gives an accurate impression of the position of the pores, even though the pores cannot be seen in the wall below.

Species with verrucose urediospores present the greatest difficulty. Neither the location nor the number of pores could be ascertained in most species of *Coleosporium*, but it is probable that all of them have several scattered pores. The spores of *Chrysomyxa* also are verrucose and have scattered pores. *C. Piperiana* has the largest number of pores of any rust studied and, while accurate counts are difficult, it is certain that there are often as many as 20.

There are three more or less distinct kinds of arrangement for the pores in the urediospores of the Melampsoraceae. All of the species in some genera have a like arrangement but in others the species may be divided into two groups (see table 1). The three arrangements may be designated as follows: (1) scattered, (2) in two fairly regular zones near the opposite ends of the spore and (3) equatorial. The arrangement may change from bizonate to scattered in spores which are nearly globoid, as previously pointed out by Moss (**31**) for *Milesia*. Most of the species of the Melampsoraceae have scattered or bizonate pores, while *Bubakia* is the only genus in which the pores are equatorial in all species.

The pores vary in number from four to twenty, with four being the characteristic number in species with equatorial pores, while five to eight is the commoner number in species with scattered pores and eight in species with two zones of pores.

Until recently the pores of the urediospores of the Melampsoraceae usually have been considered to be absent or invisible. However, Moss (**31**) studied the urediospores of *Hyalopsora*, *Milesia*, *Pucciniastrum* and *Melampsorella*, and found that pores were present and could be seen with considerable accuracy in the species studied. His observations agree in general with those of the writer. Cunningham (**13**) includes the number and position of the pores in his descriptions of the melampsoraceous species. *Chrysomyxa* is the only genus in which he found the pores to be too obscure to warrant a definite statement.

Illustrations also have given indications of the location of the pores in certain genera. For example, the figures published by Tulasne (**34**), Colley (**12**) and Bagchee (**6**) show the location of the pores for three species of *Cronartium*, and Bell's (**8**) illustrations are accurate for *Uredinopsis*. Hart (**22**) states that the pores are equatorial in *Melampsora Lini* but her illustrations do not entirely substantiate her written statement. Cunningham (**13**) also states that the pores are equatorial in *M. Lini* but during the present study they were found to be scattered, which is in agreement with other North American species of *Melampsora* and with Tulasne's (**34**) illustrations of two European species.

As a family the Melampsoraceae are characterized by urediospores with several, usually five to eight, scattered pores and by

a decided scarcity of species with equatorial pores. The arrangements of the pores are given in table 1 for the major general.

TABLE 1

THE RELATION BETWEEN THE LOCATION OF THE PORES AND THE SHAPE OF THE UREDIOSPORES IN 19 GENERA OF THE MELAMPSORACEAE AND PUCCINIACEAE

Genus	No. spp.	Average urediospore	Mean ratio of breadth to length	Arrangement of pores
Hyalopsora	2	19 × 28 μ	1 : 1.47	equatorial
	1	18 × 25	1 : 1.39	scattered
Uredinopsis	5	14 × 42	1 : 3.00	bizonate
Milesia	10	18 × 36	1 : 2.00	bizonate
Melampsoridium	3	11 × 30	1 : 2.73	bizonate
Pucciniastrum	6	14 × 19	1 : 1.36	scattered
	5	15 × 27	1 : 1.80	bizonate
Cronartium	6	18 × 25	1 : 1.38	bizonate
Chrysomyxa	9	20 × 32	1 : 1.60	scattered
Coleosporium	27	19 × 25	1 : 1.31	scattered
Melampsora	4	16 × 19	1 : 1.19	scattered
	9	19 × 30	1 : 1.58	bizonate
Phakopsora	5	17 × 23	1 : 1.35	scattered
Bubakia	2	20 × 29	1 : 1.45	equatorial
Pileolaria	4	24 × 38	1 : 1.58	equatorial
Tranzschelia	2	19 × 34	1 : 1.79	equatorial
Cumminsiella	3	19 × 31	1 : 1.63	equatorial
Uropyxis	6	18 × 25	1 : 1.38	scattered
Prospodium	6	23 × 25	1 : 1.09	equatorial
Phragmidium	15	19 × 22	1 : 1.16	scattered
Ravenelia	28	17 × 21	1 : 1.24	scattered
	26	17 × 28	1 : 1.65	equatorial
	8	16 × 26	1 : 1.63	bizonate
Puccinia	87	22 × 27	1 : 1.23	scattered
	270	22 × 28	1 : 1.27	equatorial
	3	23 × 37	1 : 1.61	bizonate

THE UREDIOSPORE-PORES OF THE PUCCINIACEAE

The arrangement and number of pores in the urediospores of the Pucciniaceae have been given so commonly that an original study was necessary for only a minority of the species. While the outer cuticular layer is hyaline the remainder of the wall is usually pigmented. Since the pigment is not deposited in the pores they are more distinct than those of the colorless urediospores of the Melampsoraceae and special treatment is usually unnecessary.

Some genera have urediospores with scattered pores only, as *Uropyxis*, *Phragmopyxis* and *Phragmidium*. *Dicheirinia*, *Tranz-*

schelia and *Prospodium* have equatorial pores. The pores are equatorial or subequatorial in *Pileolaria*, either equatorial or bizonate in *Cumminsiella*, and while difficult to observe in *Mainsia* and *Kuehneola* are probably equatorial, certainly so in some species. *Ravenelia*, *Puccinia* and *Uromyces*, all large genera, show many variations in the number and the arrangement of the pores in their urediospores, as well as diversity in other features.

As a family the Pucciniaceae are characterized by a decreasing proportion of species with scattered pores and by an increasing proportion of species with equatorial pores. When the pores are scattered the number is usually five to ten, when bizonate usually eight and when equatorial commonly two, three or four. The arrangement of the pores is given in table 1 for the major North American genera.

UREDIOSPORE-PORES AND THE SHAPE OF SPORES

There appears to be some correlation between the arrangement of pores and the shape of urediospores, in that globoid spores usually have scattered pores while ellipsoid, oblong or radially asymetrical spores usually have zonate pores. In order to demonstrate this relationship, published measurements were assembled for 552 North American species. The species in each genus were divided into groups as follows: pores scattered, pores bizonate and pores equatorial. The average spore for each species was calculated, and from the total of these averages the dimensions of the average spore for each group were obtained. To facilitate comparison between genera, or groups within genera, the mean ratios of breadth to length were calculated from the average spore of each group. The data are given in table 1.

Summarization of the table accordingly as the urediospores have scattered, equatorial or bizonate pores gives the following figures. The dimensions (to the nearest whole number) of the average urediospores are $18 \times 24\ \mu$, $20 \times 30\ \mu$ and $17 \times 34\ \mu$, and the mean ratios of breadth to length are 1 : 1.33, 1 : 1.5 and 1 : 2.0, respectively for the three groups. These data, based upon many species, indicate that the arrangement of the pores is related to the shapes of the spores, but a comparison of the above

average ratios with the ratios for individual genera shows that considerable variation may exist.

The relation between shape and arrangement of pores is fairly distinct in the genus *Ravenelia*. In the group with equatorial pores the species with the minimum variation between breadth and length has a ratio of 1 : 1.3, or equal to the maximum ratio for the species with scattered pores. The species with bizonate pores are intermediate between the group with scattered pores and the group with equatorial pores. Here the minimum ratio of breadth to length is 1 : 1.2, or equal to the average for the species with scattered pores and below the minimum for the species with equatorial pores. The maximum ratio is 1 : 2.3, a figure exceeding the average ratio for the group with equatorial pores but less than the maximum of 1 : 3.1. Such variability might be expected in a group whose individual species sometimes have pores limited to a bizonate arrangement but which have pores varying between zonate and scattered in other species, as *R. Hoffmanseggiae* and *R. Cassiae-Covesii*. The urediospores of the species with scattered pores are nearly globoid, while the species with equatorial pores are ellipsoid or oblong. This difference is distinct, as Long (**29**) has noted.

In order to have the data uniform in table 1, the species of *Puccinia* were grouped as those of the other genera. The species were placed in the equatorial-pored group unless the pores were scattered or bizonate and, as a consequence, this group is rather heterogeneous. It is possible to subdivide the equatorial group and to distinguish further variations in shape which seem rather definitely related to the position or the number of the pores.

The group most readily segregated is composed of eight species whose urediospores have the pores arranged in a ring around the hilum. The average urediospore in this group measures 23.4 $\times$ 23.6 μ and the ratio of breadth to length is 1 : 1. Here the average spore is globoid, but in some species the ratio falls to 1 : 0.88 and the spore becomes broader than high. The species with basal pores are more frequent upon the composites and the mints.

A second group can be segregated on the shape of the spores. The pores are usually two or three and equatorial or slightly be-

low. The spores are oblate-sphaeroid or reniform and usually radially asymmetrical. The average urediospore for the 18 species in this group measures 24 × 21 μ, which gives a ratio of breadth to length of only 1 : 0.88. This group of species tends to merge with the group having strictly basal pores and occurs upon the same families of hosts.

A study of the individual ratios of breadth to length for the species of *Puccinia* with equatorial pores indicated that the ratios might be smaller for the species with two pores than for the species with three or more pores. However, after removing the basal-pored and the oblate-sphaeroid groups, the ratios are the same, although the 2-pored species on the composites have a ratio of breadth to length of 1 : 1.18, or less than the average ratio for the species with scattered pores.

The above ratios of breadth to length were obtained from measurements of the urediospores with one pore in face view when the pores are two in number. An examination of the species of *Puccinia* with two pores showed that the spores are usually radially asymmetrical with the pores borne in the flattened sides. Thus, in 20 typically 2-pored species on the Carduaceae the average difference in the two diameters was found to be 4 μ when the spores were mounted in water and fully expanded. Some of the species, as *P. nuda*, *P. Cyani* and *P. cognata*, have nearly radially symmetrical spores with the diameter with pores in face view only exceeding by 1 μ that with the pores in side view. On the other hand, a difference of 6 μ was found for the urediospores of *P. turgidipes*, *P. subdecora*, *P. Balsamorrhizae* and others. Such urediospores are decidedly asymmetrical. Thus in *P. Balsamorrhizae*, for example, if a line were drawn through the two pores the diameter as measured on that line would be 21 μ, but if measured on a line at right angles to the pores the diameter would be 27 μ. Even in species which have symmetrical or nearly symmetrical spores the wall is usually flattened or indented around the pore and the apparent uniform curvature of the wall is due to a cuticular umbo which fills this invagination. In *P. Plucheae*, for example, the diameter through the pores is 25 μ and only 26 μ in the opposite plane, when the spores are mounted in water, but one-third of the 25 μ is due to the cuticular umbo. *P.*

Plucheae is an extreme example of the kind of spore commonly exhibited by species with only two equatorial pores.

The ratios of breadth to length, given in table 1, are dependable for the urediospores with scattered pores but are misleading for the groups which contain the two-pored species because the differences responsible for the shapes of such spores are three-dimensional.

The preceding data and observations do not lend themselves to concise tabulation. Nevertheless, certain general conclusions seem possible. Radially symmetrical, nearly globoid urediospores are characterized by scattered pores, varying in number from five to ten or more. Urediospores with equatorial pores, usually two to four in number, are ellipsoid or oblong or when seemingly globoid are radially asymmetrical with the pore-bearing sides flattened. Oblate-sphaeroid spores are also radially asymmetrical and show a tendency to have subequatorial or basal pores. Urediospores with bizonate pores are ellipsoid or oblong and tend to have scattered pores when individual spores become more nearly globoid. The pores are usually eight in number.

UREDIOSPORE-PORES AND THE PIGMENTATION OF THE WALL

The statements which follow demonstrate that there is a correlation between the arrangement of pores and the pigmentation of the walls of the urediospores. Spores with scattered pores usually have colorless walls while spores with few equatorial pores tend to have strongly pigmented walls.

The Melampsoraceae are characterized by urediospores with little or no color in the walls. In *Melampsora*, especially the autoecious species, some slight coloration is evident and the same is true of *Crossopsora*, *Phakopsora* and *Angiopsora*. On the other hand, the urediospores of *Bubakia* are definitely brown and resemble those commonly present in *Puccinia*. The melampsoraceous rusts are conspicuous by their failure to develop urediospores with equatorial pores. *Bubakia* has equatorial pores, but the position which the genus merits in a natural classification is open to question. It is notable that those genera which are assigned to the Melampsoraceae and whose taxonomic position is

least disputed are those with the least pigment in the walls of the urediospores.

No such uniformity exists in the Pucciniaceae. *Phragmidium* and *Uropyxis* are examples of pucciniaceous genera having urediospores with nearly colorless walls and several scattered pores. On the other hand, the urediospores of *Pileolaria*, *Cumminsiella*, *Tranzschelia*, *Dicheirinia*, *Ravenelia*, *Puccinia*, *Uromyces* and in part those of *Prospodium* show a distinct pigmentation. It is also striking that the species in the genera *Pileolaria*, *Cumminsiella*, *Tranzschelia*, *Dicheirinia* and *Prospodium* have equatorial pores. In *Ravenelia* 26, or 42 per cent, of the species have equatorial pores, while in the combined genera *Puccinia-Uromyces* 75 per cent of the species have equatorial pores. It is also noteworthy that many species of *Puccinia* which have urediospores with nearly colorless walls also have scattered pores, as *P. rubigo-vera*, *P. coronata*, *P. glumarum*, *P. conspicua*, *P. Liatridis*, *P. Eatoniae*, *P. Poae-sudeticae*, *P. Blasdalii*, *P. Oxalidis* and *P. evadens*.

The above statements show that the development of pigment in the walls of urediospores has been rather consistently paralleled by the development of an equatorial rather than a scattered arrangement of pores. There is an accompanying reduction in the number of pores, since the number is less when the pores are equatorial. It seems that an increase in the pigmentation of the walls is a factor in increasing the resistance of spores to adverse climatic conditions.

It is notable in this regard that the walls of teliospores which germinate after overwintering are deeply pigmented, as those of *Melampsora*, *Phragmidium*, *Puccinia* and *Uromyces*. On the other hand, the teliospores of *Coleosporium*, *Mainsia*, *Acrotelium*, *Maravalia* and *Cronartium* have colorless or nearly colorless walls and germinate without an extended period of "rest." There are exceptions in both categories. In the *lepto*-species of *Puccinia* there are often two kinds of teliospores, one pale and capable of immediate germination (*forma persistens*), the other darker and capable of overwintering (*forma fragilipes*). Dietel (**14**) and Jørstad (**27**) have discussed such species.

Present information indicates that pigmentation of the walls of

aeciospores is also associated with an increased ability to remain viable during exposure to climatic extremes. The studies by Fukushi (**20**) with *Gymnosporangium Yamadae* and by Miller (**30**) with *G. Juniperi-virginianae* prove that the pigmented spores of these two species are more resistant to exposure than are the paler spores of *G. Haraeanum* (**20**).

Published data regarding the longevity of urediospores are conflicting but one paper indicates that the pigmentation of the walls of urediospores serves in a protective capacity. By using the color mutants discovered by Newton and Johnson (**32**) in *Puccinia graminis Tritici*, Dillon Weston (**18**) proved that the normally pigmented walls are more resistant to ultra-violet radiation than are the mutants lacking the pigment.

Species which develop amphispores in addition to ordinary urediospores offer further examples indicating that pigmentation serves in a protective capacity. The amphispores are more deeply pigmented than the urediospores in such species and often have fewer pores. For example, the urediospores of *Puccinia vexans* have several scattered pores while the amphispores have three or four equatorial pores. Urediospores and teliospores are not formed in abundance in amphisporic rusts, the amphispores serving to preserve the species through the winter, as Carleton (**11**) proved experimentally with *P. vexans*. Amphisporic species are probably capable of existing independent of an alternate host for indefinite periods. The amphispore, an adaptive modification of an urediospore, makes this possible.

The evident changes which have given rise to amphispores have been a thickening of the wall, an increase in pigmentation and often a decrease in the number of pores. Since amphispores have persistent pedicels their importance as disseminating agents has become secondary, and they have assumed one of the functions and some of the morphology of teliospores. Urediospores which have the same pigmentation of the walls but which have retained easily disjoined pedicels must also have increased their chance of survival, but without diminishing their capabilities for dissemination.

UREDIOSPORE-PORES AND UREDIAL PERIDIA AND PARAPHYSES

The presence of peridia or paraphyses is characteristic of the uredia of many species, and is correlated with the scattered arrangement of pores in the urediospores. It was pointed out above that the Melampsoraceae have urediospores with several scattered pores and unpigmented walls. The formation of a peridium is also a development common to most of these rusts. Thus a peridium is present in *Uredinopsis*, *Milesia*, *Hyalopsora*, *Melampsoridium*, *Pucciniastrum*, *Cronartium* and *Chrysomyxa*. The species of *Melampsora* are conspicuous for the development of numerous paraphyses, while in *Phakopsora* the uredia may have paraphyses or these may be united at their base to form a peridium. Neither peridia nor paraphyses are present in *Coleosporium*. They also are wanting in *Bubakia*, but as indicated before this genus deviates from other genera of the Melampsoraceae.

A peridium, as formed in the Melampsoraceae, is no longer present in the Pucciniaceae and, while paraphyses characterize certain genera, a majority of the species of the family have neither. A change in the arrangement of the pores from scattered to equatorial has occurred more or less in parallel with the elimination of peridia and paraphyses.

Paraphyses are present in all of the species of *Tranzschelia* and *Phragmidium*, in most of the species of *Uropyxis*, *Dicheirinia* and *Prospodium*, in about one-third of the species of *Ravenelia* and *Cumminsiella*, in a minority of the species of *Puccinia* and *Uromyces* and in none of the species of *Pileolaria*. The species of *Phragmidium* and *Uropyxis* have urediospores with scattered pores. The pores are equatorial in *Tranzschelia*, *Dicheirinia*, *Prospodium* and *Pileolaria* and equatorial or bizonate in *Cumminsiella*. Of the species of *Ravenelia* studied 20 of 28 (71 per cent) which have scattered pores also have paraphyses, 16 of 26 (61 per cent) which have equatorial pores have paraphyses, and 6 of 8 (75 per cent) which have bizonate pores also have paraphyses. In the genus *Puccinia* 20 species were found to have paraphyses. Of this 20, 65 per cent have urediospores with scattered pores and the species occur almost exclusively upon the grasses.

This summary again serves to emphasize that the urediospores and their sori have experienced a parallel evolution. It is significant that the more primitive genera have retained peridia or paraphyses, which probably serve a protective function according to Dietel (**15**), Arthur *et al* (**3**) and Grove (**21**), but that in the more advanced genera, especially *Puccinia*, these structures have been all but eliminated. It is also significant that most of the urediospores developed in these protected sori have scattered pores and colorless or nearly colorless walls.

Such a consistent trend indicates that the retention of protective structures in the sorus became unnecessary as the pigment in the walls increased and the number of pores decreased. Or it may be that the loss of protective structures came first and that those species survived which compensated this loss by the development of urediospores with more pigment and with fewer pores.

The change from a peridium to paraphyses is more or less paralleled by an increase in the length of the pedicels of the urediospores. A peridium is well developed in the Pucciniastreae and the urediospores are nearly sessile. Where paraphyses are present but the peridial tissue absent, as in *Ravenelia* and *Puccinia*, the urediospores have definite, well differentiated pedicels. This parallelism is to be expected since peridial cells and paraphyses are metamorphosed spore-initials. As the urediospores develop pedicels the tendency is also toward the production of stipitate paraphyses rather than a cellular peridium.

UREDIOSPORE-PORES AND THEIR RELATION TO OTHER CHARACTERISTICS OF THE RUSTS

The data in preceding sections show rather clearly that several scattered pores is a condition characteristic of the urediospores of the more primitive genera and that urediospores with few equatorial pores increase in frequency in the more advanced genera. The following data demonstrate that the scattered arrangement of pores is also correlated with other characters generally conceded to be primitive.

Because of the large number of species and the diversity of life cycles and of hosts the following data deal mainly with *Puccinia*

and *Uromyces*, with reference made to other genera when pertinent to the discussion. Since *Puccinia* and *Uromyces* are retained as separate genera only for convenience they were merged in compiling most of the data. Only species with uredia are considered.

THE RELATION OF POSITION OF UREDIOSPORE-PORES TO HETEROECISM AND AUTOECISM

A study of the species of *Puccinia-Uromyces* of known life cycle shows that a relationship exists between the arrangement of the pores in the urediospores and heteroecism and autoecism. The data are given in table 2.

TABLE 2

THE RELATION OF NUMBER AND ARRANGEMENT OF PORES IN THE UREDIOSPORES TO HETEROECISM AND AUTOECISM IN *Puccinia-Uromyces*

Arrangement of pores	Heteroecious		Autoecious	
	Species	Per cent	Species	Per cent
Scattered	37	43	35	18
Equatorial	49	57	162	82
Pores 3+	32	65	84	52
Pores 2	16	33	76	47
Pores 1	1	2	2	1

The data in table 2 demonstrate that the scattered arrangement of pores is possessed more frequently by heteroecious species than by autoecious species, and that a marked majority (82 per cent) of the autoecious species have equatorial pores. Since pores when equatorial are usually fewer in number than when scattered, it follows that autoecious species tend to have fewer pores in the urediospores than do heteroecious species. It should also be noted that a greater proportion of the heteroecious species with equatorial pores have three or more pores than do the autoecious species.

Although some of the autoecious genera of the Pucciniaceae (*Uropyxis*, *Phragmopyxis* and *Phragmidium*) have urediospores with scattered pores only, it is notable that the species of the Melampsoraceae are heteroecious and that none have equatorial

pores except *Hyalopsora* and *Bubakia*, the latter with life cycle unknown.

This analysis shows that the change in the arrangement of the pores in urediospores tends to parallel the change from heteroecism to autoecism, in that the scattered arrangement is more common in heteroecious than in autoecious species. Since heteroecism is usually believed to be a more primitive condition than autoecism [Blackman (**9**), Arthur (**1**), Orton (**33**), Jackson (**26**)] it is evident that urediospores with scattered pores are significantly associated with the more primitive type of life cycle.

THE RELATION OF POSITION OF UREDIOSPORE-PORES TO AECIA

A considerable number of the species of *Puccinia-Uromyces* have uredinoid rather than aecidioid aecia and a tabulation of the species demonstrates that there is a correlation between the arrangement of the pores in the urediospores and the kind of aecia. A greater proportion of the species with aecidioid than with uredinoid aecia have scattered pores. Only species of known life cycle are used. The data are given in table 3.

TABLE 3

THE RELATION OF NUMBER AND ARRANGEMENT OF PORES IN THE UREDIOSPORES TO THE AECIA IN *Puccinia-Uromyces*

Arrangement of pores	Aecia aecidioid		Aecia uredinoid	
	Species	Per cent	Species	Per cent
Scattered	67	32	5	7
Equatorial	143	68	68	93
Pores 3+	82	57	34	50
Pores 2	59	41	33	49
Pores 1	2	2	1	1

The data in table 3 show that the change in the arrangement of the pores in the urediospores has rather closely paralleled a change in the aecia. Urediospores with scattered pores and aecia that are aecidioid are more often associated than are scattered pores and uredinoid aecia, while 93 per cent of the species with uredinoid aecia have urediospores with equatorial pores. A study of the species which have three or more equatorial pores or only

two equatorial pores gives little that is significant (table 3). The differences are too small to allow the prediction that species with uredinoid aecia and equatorial pores tend toward a reduction in the number of pores.

With the preceding results in mind a study was made of the distribution of species having the various arrangements of pores, according to whether the species are heteroecious with aecidioid aecia, or autoecious with aecidioid or uredinoid aecia. No known heteroecious species has uredinoid aecia. The results are given in table 4.

TABLE 4

THE DISTRIBUTION OF SPECIES OF *Puccinia-Uromyces* ACCORDING TO THE AECIA, HETEROECISM, AUTOECISM AND ARRANGEMENT OF PORES IN THE UREDIOSPORES

Arrangement of pores	Heteroecious			Autoecious			
	Aecidioid		Uredinoid	Aecidioid		Uredinoid	
	Species	Per cent	Species	Species	Per cent	Species	Per cent
Scattered	37	43	0	30	24	5	7
Equatorial	49	57	0	94	76	68	93
Pores 3+	32	65	0	50	53	34	50
Pores 2	16	33	0	43	46	33	49
Pores 1	1	2	0	1	1	1	1

The data in table 4 show that species which have urediospores with scattered pores are more commonly heteroecious than autoecious, and more commonly have aecidioid than uredinoid aecia. Species with equatorial pores are autoecious more commonly than heteroecious. Although more species have aecidioid than uredinoid aecia, yet a greater proportion of those with uredinoid aecia have urediospores with equatorial pores than do those with aecidioid aecia. In the last three lines of table 4 the equatorial group is divided into subgroups, as in tables 2 and 3. The differences are not great but show a consistent trend, in that there seems to be some tendency toward a decrease in the number of pores as the life cycle changes from heteroecious to autoecious and the aecia from aecidioid to uredinoid.

Unfortunately the life cycles of the species of *Ravenelia* are too poorly understood to offer substantial evidence on this point.

It is known that the aecia may be aecidioid or uredinoid, according to the species considered, and perhaps most have uredinoid aecia. The aecia are uredinoid in the genus *Uropyxis* and the pores in the urediospores are scattered. On the other hand, uredinoid aecia occur in *Dicheirinia*, *Maravalia*, *Pileolaria*, *Uromycladium*, *Prospodium*, *Mainsia*, *Kuehneola*, and probably *Hapalophragmium* and *Sphaerophragmium*, all genera having urediospores with few equatorial pores in most and perhaps in all species. There are no species known to have uredinoid aecia in the Melampsoraceae and none have equatorial pores, except *Bubakia* and some species of *Hyalopsora*.

Jackson (**26**) has presented evidence that aecidioid aecia are more primitive than uredinoid aecia, a belief previously implied in Arthur's (**2**) life cycle classification. The relationship, shown in tables 3 and 4 between urediospores with scattered pores and aecidioid aecia, again demonstrates that the scattered arrangement of pores tends to be significantly correlated with primitive characters. The opposed, or equatorial arrangement, is almost exclusively present in species having the more recent uredinoid type of aecium.

UREDIOSPORE-PORES AND ARTHUR'S CLASSIFICATION OF PUCCINIA-UROMYCES

In addition to the preceding data Arthur's (**4**) classification of *Puccinia-Uromyces* is important. He has made the only attempt, based upon a large flora, to separate the species into phylogenetic groups. The separation is based partly upon the kind of aecia but more especially upon the morphology of the teliospores. Arthur considers the section *Eupuccinia* to contain the more primitive species and the section *Bullaria* the more recent species.

Arthur's (**4**) Manual contains 304 species of *Puccinia-Uromyces* which have uredia. A tabulation of the two sections shows that 71 of the 202 species in *Eupuccinia* have scattered pores and that 131 have equatorial pores, or 35 per cent and 65 per cent, respectively. Similar tabulation of the section *Bullaria* shows that 20, or 20 per cent, of the 102 species have urediospores with scattered pores while 82, or 80 per cent, have equatorial pores.

Since Arthur's classification is based upon the morphology of

the teliospores it is evident that the arrangement of the pores in the urediospores of *Puccinia-Uromyces* tends to change in parallel with changes in the morphology of the teliospores. Urediospores with several scattered pores are most often associated with teliospores which are oblong, have smooth, apically thickened walls, persistent pedicels and the pore of the lower cell at the septum (§ *Eupuccinia*). Urediospores with few equatorial pores are most often associated with teliospores which are ellipsoid, have sculptured, uniformly thickened walls, fragile pedicels and the pore of the lower cell tending toward the pedicel (§ *Bullaria*). In other words, urediospores with scattered pores tend to be associated with primitive teliospores.

THE RELATION OF POSITION OF UREDIOSPORE-PORES TO HOSTS

Having found that the arrangement of pores in the urediospores is related to heteroecism, autoecism and the aecia, figures were compiled which demonstrate that there is a general correlation with the groups of hosts. The data are presented in table 5 and are based upon species of *Puccinia* with known life cycles.

TABLE 5

THE RELATION OF THE ARRANGEMENT OF UREDIOSPORE-PORES IN THE GENUS *Puccinia* TO THE GROUPS OF HOSTS

Hosts	Aecia aecidioid				Aecia uredinoid			
	Scattered		Equatorial		Scattered		Equatorial	
	Species	Per cent	Species	Per cent	Species	Per cent	Species	Per cent
Monocots	34	46	40	54	0	0	0	0
Dicots	10	14	64	86	4	6	61	94
Archichl.	5	23	17	77	3	16	16	84
Metachl.	5	10	47	90	1	2	45	98

A definite relationship apparently exists here (table 5), and since the data in table 3 proved that the species of *Puccinia-Uromyces* with uredinoid aecia show a preponderance of urediospores with equatorial pores over those with aecidioid aecia, it becomes apparent that the proportion of species with scattered pores is greater on the monocotyledonous hosts. Not only has a

greater proportion of the species of *Puccinia* on the Dicotyledoneae developed equatorial pores but the two subgroups within the dicotyledons differ in this respect. The species on the Metachlamydeae considerably exceed those on the Archichlamydeae and, in those with uredinoid aecia, comprise 98 percent of the species.

A segregation of the data providing the basis for table 5, to account for heteroecism and autoecism, brings out further interesting figures, which are given in table 6.

TABLE 6

THE RELATION OF HETEROECISM, AUTOECISM AND ARRANGEMENT OF PORES IN THE UREDIOSPORES TO THE MAJOR GROUPS OF HOSTS FOR THE GENUS *Puccinia*

Hosts	Pores scattered				Pores equatorial			
	Heteroecious		Autoecious		Heteroecious		Autoecious	
	Species	Per cent	Species	Per cent	Species	Per cent	Species	Per cent
Monocots.....	27	79	7	21	35	87	5	13
Dicots.....	3	21	11	79	2	2	123	98
Archichl....	3	38	5	62	2	6	31	94
Metachl....	0	0	6	100	0	0	92	100

The data in table 6 show that the species of *Puccinia* on the monocotyledons are more apt to be heteroecious than autoecious, while those on the dicotyledons are more apt to be autoecious than heteroecious. Likewise, the species on the Archichlamydeae are more apt to be heteroecious than are those on the Metachlamydeae.

A total of 213 species is included in table 6, 74 on the monocotyledons and 139 on the dicotyledons. Of those on the monocotyledons 54 per cent have equatorial pores, but the pores are equatorial in 90 per cent of the species on the dicotyledons. Likewise, 80 per cent of the species on the Archichlamydeae have equatorial pores while the pores are equatorial in 94 per cent of the species on the Metachlamydeae.

Arranging the grass rusts of North America according to the system of tribes in the Poaceae, as presented by Hitchcock (**23**), shows that a more or less consistent trend exists among the grass

rusts, *Puccinia-Uromyces*. Species with scattered pores are more frequent on the primitive tribes and decrease in abundance on the advanced tribes. Species with equatorial pores are rare on the primitive tribes and more numerous on the higher tribes. This is shown graphically in figure 1.

Grass tribe	Pores equatorial	Pores scattered
Bamboseae	xxx	
Festuceae	xxx	xxxxxxxxxxxxxxxxxxxxx
Hordeae	x	xxxxxxxxx
Aveneae	x	xxxxxxxxxx
Agrostideae	xxxxxxxxxxx	xxxxxxxxxxxxxxxxxxx
Nazieae		xxx
Chlorideae	xxxxxx	xxxxxxxxxx
Phalarideae	x	xx
Oryzeae	x	
Paniceae	xxxxxxxxxxxxxxx	xxxxxx
Andropogoneae	xxxxxxx	xxxx
Tripsaceae	xxxx	

Fig. 1. The relation between the arrangement of urediospore-pores and the host tribes for the North American grass rusts, *Puccinia-Uromyces*. Each x represents one species.

The above data show that there is a general correlation, in the genera *Puccinia* and *Uromyces*, between the arrangement of the pores in the urediospores and the taxonomic position of the hosts parasitized. Species with scattered pores are more frequent on the Archichlamydeae than on the more advanced Metachlamydeae and more frequent on the primitive than on the advanced tribes of the grasses. A greater proportion of the species on the Monocotyledoneae than on the Dicotyledoneae have scattered pores and, since the Monocotyledoneae are thought to have been derived from the Dicotyledoneae (see Hutchinson, **25**), the general correlation does not hold with respect to the species on the monocotyledons.

DISCUSSION AND CONCLUSIONS

The differences which exist between the uredia and urediospores of the Melampsoraceae and the Pucciniaceae have been reviewed in some detail. The melampsoraceous species have uredia with peridia or paraphyses and urediospores with colorless or nearly colorless walls and several scattered pores. Exceptions were pointed out. The Pucciniaceae have uredia with no peridia

and in the majority of species with no paraphyses. While diverse in the various genera and species the walls of the urediospores are usually pigmented and provided, in a consistent majority, with few equatorial pores. The species which have paraphyses more commonly have spores with scattered pores and colorless wall than with equatorial pores and a pigmented wall. A specialization in the shape of urediospores with equatorial pores also was indicated. Correlations were shown to exist between the scattered arrangement of urediospores and heteroecism and aecidioid aecia, and between equatorial pores and autoecism and uredinoid aecia. Primitive teliospores in *Puccinia* and *Uromyces* are more apt to be associated with urediospores with scattered than with equatorial pores. Moreover, the primitive groups of hosts support a greater proportion of species with scattered than with equatorial pores while the advanced groups of hosts support a preponderance of species with equatorial pores.

Such a consistent association of the scattered arrangement of pores with other characters conceded to be primitive leads to the conclusion that *several scattered pores represent the primitive condition for urediospores*. Otherwise one is reduced to considering that the evolution of the uredia and their spores has proceeded independently of the evolution of species. Since the evolutionary sequence of genera and species can only be decided by changing morphology the two cannot well be divorced.

If one chooses to base interpretations upon telia only, one cannot avoid recognizing parallel development, since urediospores with scattered pores and colorless walls, and uredia with peridia or paraphyses occur in the genera which have teliospores in laterally adherent crusts. Even the species of *Puccinia* which have indehiscent, compact telia also commonly have urediospores with scattered pores, as *P. coronata*, *P. Eatoniae*, *P. Koeleriae*, *P. Liatridis*, *P. glumarum*, *P. Hordei*, *P. anomala*, *P. Blasdalii*, *P. Porri*, *P. granulispora* and *P. subangulata*. Some of these species also have uredial paraphyses and, so far as known, all are heteroecious except the last four.

Aside from the change from several scattered pores to few equatorial pores there is evidence that the tendency to reduce the number of pores is continued within the equatorial-pored species

of *Puccinia-Uromyces*. The data in table 2 show that a greater proportion of the heteroecious than of the autoecious species have three or more pores. Following table 3 it was pointed out that more of the species with aecidioid aecia have three or more pores than do the species with uredinoid aecia. Furthermore, table 4 shows that the proportion of three-pored species decreases from a maximum in the heteroecious aecidioid group through the autoecious aecidioid group to its minimum in the autoecious uredinoid group. Although the differences are not great the trend appears to be consistently toward fewer pores.

It was pointed out that the arrangement of the pores in urediospores tends to change with the changing morphology of the teliospores in *Puccinia-Uromyces*. Nevertheless, some species whose telia indicate recent development have retained uredia and urediospores of the primitive type. No species is more anomalous than *Puccinia paradoxica*. This rust has specialized teliospores, typical of Arthur's section *Bullaria*, yet the uredia have paraphyses and the urediospores have scattered pores and a nearly colorless wall. The complete life cycle is not known. Species with such teliospores are usually autoecious but there are exceptions, as *P. Bistortae*. Some species of *Uromyces* on fabaceous hosts also have *Bullaria*-like teliospores but urediospores with scattered pores, and are heteroecious, as *U. occidentalis* and *U. punctatus*. While these species have teliospores of a specialized type they have retained the more primitive life cycle and arrangement of pores in the urediospores.

There are also autoecious species with teliospores of the primitive type of Arthur's section *Eupuccinia* but with urediospores having two equatorial pores. *Puccinia Helianthi* is a common species of this kind. *P. Helianthi*, however, appears to be of unstable life cycle and sometimes forms pycnia and aecidioid aecia but occasionally has pycnia associated with uredia (uredinoid aecia), as discovered by Carleton (**11**) and verified by Bailey (**7**). In addition to having urediospores with two equatorial pores the species seems then, also to be tending toward a change from aecidioid to uredinoid aecia. Jackson (**26**) has pointed out that the autoecious *Puccinia orbicula* likewise has an unstable life cycle, with pycnia and aecidioid aecia sometimes associated or

with pycnia occurring with the uredia in other cases. While the teliospores of *P. orbicula* are typical of the section *Bullaria* the pores of the urediospores are not equatorial. Nevertheless, the number of pores is variable, sometimes only two or three, and the urediospores seem unstable as well as the aecia.

While not all morphologic characters change strictly in parallel the tendency in *Puccinia* seems to be toward parallel changes which would ultimately yield autoecious species with uredinoid aecia, teliospores with uniformly thick, sculptured walls, fragile pedicels (and perhaps with the pore of the lower cell near the pedicel) and urediospores with few equatorial pores, provided that the aecia and uredia are not eliminated during the course of evolution. This appears to happen with increasing frequency as this theoretically ultimate morphology is approached, as is pointed out below.

It is interesting to note that Hutchinson (**24**), in stating the "general principles adopted for the classification of plants," includes as his first three dicta rules which apply to the rusts. The three dicta are: (1) evolution is both upwards and downwards, the latter involving degradation and degeneration; (2) evolution does not necessarily involve all organs of the plant at the same time, and one organ or set of organs may be advancing whilst another set is stationary or retrograding; (3) evolution has generally been consistent, and when a particular progression or retrogression has set in, it is persisted in to the end of the phylum.

It is probable, because of the strict parasitism of the rusts, that evolution has generally been toward simplification rather than toward amplification, as evidenced by the simplification of life cycles, reduction in the number of pores in the urediospores and loss of uredial paraphyses, and perhaps upward through the production of a protective coloration and greater adaptation for dissemination. Kern (**28**) and Orton (**33**) have pointed out that parasitism may account for the tendency toward simplification of life cycles. It has been mentioned in this paper that evolution has not involved all characters at the same time, but it was also pointed out that the changes in the pores of the urediospores and other features peculiar to the sorus and its spores have been remarkably consistent.

There is also evidence that the changes in the morphology of the teliospores, which were discussed above, have followed through the genera *Puccinia* and *Uromyces* consistently, and that the changes have been paralleled by a progressive simplification of the life cycle. For example, in the section *Eupuccinia*, less than one-third (85 species = 29 + per cent) of the species have lost the uredia or the aecia or both, but in the section *Bullaria* one-half (98 species = 49 + per cent) of the species have become demicyclic or microcyclic.

Data presented in tables 5 and 6 indicate that the monocotyledons have remained a more primitive group than the dicotyledons. Although questions of phylogeny are open to controversy the view that the monocotyledons are more primitive than the dicotyledons does not have the support of phanerogamic taxonomists (see Hutchinson, **25**). However, it is not so much a question of whether the monocotyledons have been derived from the dicotyledons as of which of the two groups has progressed the farther from the original type. In other words, while the monocotyledons may have been derived from the lower orders of the dicotyledons, they may still contain fewer recently developed orders and families than the dicotyledons. The important factor here is the relative ages of the various hosts, rather than the point of origin of the two major groups. It would be strange if the otherwise consistent trends brought out in this paper should fail only with respect to the monocotyledonous hosts. It is not the purpose of this paper to question the phylogeny of the angiosperms but it is permissible to follow to its logical conclusions the theory that the scattered arrangement of several pores is the primitive condition for urediospores. On that basis the conclusion is justified that the species of *Puccinia-Uromyces* which inhabit the monocotyledons are more primitive, on the whole, than are those which inhabit the dicotyledons.

Even though the morphologic characters of the rusts change more or less in parallel, the variability is still such that it is difficult to choose characters of taxonomic value, although the differences, or more correctly the similarities, in morphology furnish the evidence upon which relationships are based. Classifications are based primarily upon the telia and teliospores, and correctly

so, but a natural system cannot be attained with the use of a single spore-form. For that reason the present study should aid in reaching a more natural grouping, which is the major aim of taxonomic work. While no attempt has been made to construct a natural classification the application of the data in this paper may indicate the relationship of genera and species to some extent.

Beginning with the Melampsoraceae it is logical to consider that the Pucciniastreae represent a closely related group of genera, since all have uredia and urediospores with similar characters; all have peridia and a like arrangement of pores. This relationship has not been doubted. *Melampsora* shows relationship to the Pucciniastreae through the species on *Salix* and has probably given rise in turn, through the autoecious species with slightly pigmented urediospores, to *Bubakia*, which represents the highest development of the Melampsoraceae.

Although *Crossopsora* is usually thought to be closely related to *Cronartium* this seems unlikely, since the uredia have paraphyses rather than peridia and the urediospores have equatorial pores and pigmented walls. The shape of the spores is rather specialized in some species of *Crossopsora*, which is not true of *Cronartium*. It is probable that, while the telia have developed in parallel, the genera may have little direct relationship.

Within the Pucciniaceae uredia may be used as an index of relationships in some cases. For example, *Ravenelia* appears to have served as a point of origin for several smaller genera which have urediospores of specialized shape and sculpture and few, often one or two, equatorial or basal pores. These genera are *Sphaerophragmium*, *Hapalophragmium*, *Dicheirinia*, *Diorchidium* and *Uromycladium*. I consider that these genera are derivatives of *Ravenelia* rather than the reverse, as Dietel's (17) classification implies, because all of them have urediospores with equatorial pores. Other features, such as the reduction in the complexity of the teliospore-heads, likewise favor this arrangement.

Dicheirinia, *Hapalophragmium* and *Sphaerophragmium* have characteristic, radially asymetrical urediospores so similar that the genera can be separated accurately only with the aid of telial characters. The urediospores of these three genera indicate a closer relationship to *Ravenelia* than to *Uromycladium*. The

sculpturing of the walls and the arrangement of the pores in the urediospores of *Uromycladium* is so similar to that of *Pileolaria*, on the other hand, as to indicate a relationship, especially through such a species as *P. phyllodiorum*, as Dietel (**16**) has suggested. Although a relatively unknown genus, *Maravalia* is evidently related to *Pileolaria* and *Uromycladium*. Dietel (**17**) states that the urediospores are spindle form and warted in *M. hyalospora* and I have found (in *M. utriculata* Syd.?) that the aecia are uredinoid with striately sculptured aeciospores having equatorial pores, and that the pycnia are subcuticular. These are characters also found in *Pileolaria*.

Since classifications of single genera usually follow the families of hosts the relationship of species is often obscured. This is desirable for convenience but makes the arrangement of species artificial. In the genus *Puccinia*, for example, the species on grasses are arranged according to the genus or tribe (often alphabetically) which serves as the telial host. This often separates species having common characters, as *P. pygmaea*, *P. coronata*, *P. Eatoniae*, *P. Koeleriae*, *P. Liatridis*, *P. conspicua*, *P. Poae-sudeticae*, *P. Piperi*, *P. procera*, *P. montanensis*, *P. rubigo-vera*, *P. glumarum*, *P. Hordei*, *P. anomala*, *P. sessilis*, *P. Cockerelliana* and *P. Poarum*, all species having urediospores with only slightly pigmented walls and several scattered pores, and several of which have uredial paraphyses. The telia are also similar, being indehiscent and paraphysate with teliospores with short pedicels, a wall not greatly thickened apically and often paler in color than those in dehiscent exposed telia. If Arthur (**4**) had followed more closely the arrangement of the grass tribes presented by Hitchcock (**23**) the sequence of the species of *Puccinia-Uromyces* would correspond more closely to their relationships. The species with nearly colorless urediospores with scattered pores and with indehiscent telia would start the sequence and gradually be replaced by species with pigmented, equatorial-pored urediospores and erumpent dehiscent telia. This was demonstrated in figure 1 with respect to the arrangement of pores.

The rusts on the Cyperaceae are a relatively homogeneous group with a tendency toward urediospores with superequatorial pores and an almost complete absence of species with scattered

pores (*P. karelica*). These characters set them off rather sharply from the rusts on grasses and indicate a relationship with the rusts on Juncaceae.

Although such groups of species as those mentioned above appear to be interrelated there is a practical limit to the number of sections into which a genus can be divided without creating confusion, thereby defeating the primary purpose of such subdivisions, *i.e.*, to indicate relationships.

It is open to question in how far the use of urediospores or uredia is justified in classifications. It seems probable that they may furnish the characters by which certain genera, as *Cerotelium* and *Kuehneola*, *Cronartium* and *Crossopsora* for example, can be satisfactorily distinguished. However, the segregation or aggregation of species according to the arrangement of the pores in the urediospores can only be advantageous when other morphologic features are also considered.

An attempt to construct a classification including all genera and giving due consideration to the uredia and their spores will provide the real test of the data presented in this paper. This, to be successful, must await more complete information regarding many poorly understood genera, and would be aided by studies, similar to the present one, in other regions and on other morphologic characters. A system to be of phylogenetic significance should be based upon entire plants, and the more complete the available information the better the system will be.

SUMMARY

1. The data presented in this paper clearly indicate that the scattered arrangement of several pores is the primitive condition for urediospores, since such spores are: (1) commoner in the Melampsoraceae than in the Pucciniaceae, (2) not specialized in shape, (3) usually provided with colorless or nearly colorless walls, (4) commonly produced in uredia having peridia or paraphyses, (5) significantly associated, in *Puccinia-Uromyces*, with heteroecism, aecidioid aecia and primitive teliospores, and (6) tend to predominate on the more primitive groups of hosts of the genera *Puccinia* and *Uromyces*. The equatorial arrangement of few pores is correlated with the opposed character in each of the

above categories, which indicates that it is an advanced character, phylogenetically.

2. There is no evidence indicating that these changes have been detrimental, and the decrease in the number of pores and the increase in pigmentation are believed to increase the longevity of the spores. It is also suggested that the loss of uredial peridia and paraphyses, believed by previous writers to be protective structures, has been compensated by the development of urediospores with pigmented walls and fewer pores.

3. The present tendency in *Puccinia-Uromyces* appears to be toward parallel changes which would ultimately yield autoecious species with uredinoid aecia, urediospores with few equatorial pores, and teliospores with uniformly thick, sculptured walls and fragile pedicels. The aecia and uredia have been eliminated with increasing frequency as this theoretically ultimate morphology has been approached.

4. Judged on the basis of the arrangement of urediospore-pores the Pucciniastreae appears to be a closely related group of genera which has probably given rise to *Melampsora* and *Bubakia*. *Crossopsora* and *Cronartium* do not seem to be as closely related as usually assumed. It is likely that *Ravenelia* has given rise to *Sphaerophragmium*, *Hapalophragmium*, *Dicheirinia*, *Diorchidium* and *Uromycladium*, rather than the reverse, while *Uromycladium* appears to be the parent stock for *Pileolaria* and *Maravalia*. Within the grass rusts of the genera *Puccinia* and *Uromyces* a natural arrangement would begin with species having nearly colorless urediospores with scattered pores and indehiscent telia and gradually extend to species having such advanced characters as pigmented, equatorial pored urediospores and erumpent dehiscent telia.

5. The data are in agreement with the general belief that evolution in the rusts has been toward simplification and reduction.

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LITERATURE CITED

1. **Arthur, J. C.** Fern rusts and their aecia. Mycologia **16**: 245–251. 1924.
2. ——. Uredinales. N. Am. Flora **7**: 85–848. 1907–1927.
3. —— (in collaboration with F. D. Kern, C. R. Orton, F. D. Fromme, H. S. Jackson, E. B. Mains, G. R. Bisby). The Plant rusts (Uredinales). pp. i–v, 1–446. New York, John Wiley & Sons. 1929.

4. ——. Manual of the rusts in United States and Canada. pp. i–xv, 1–438. Lafayette, Ind., Purdue Research Foundation. 1934.
5. —— **& F. D. Fromme.** The taxonomic value of pore characters in the grass and sedge rusts. Mycologia **7**: 28–33. 1915.
6. **Bagchee, K.** Investigations on the infestation of *Peridermium himalayense* Bagchee, on *Pinus longifolia*. II. Indian Forest Records Bot. **18**: 1–66. 1933.
7. **Bailey, D. L.** Sunflower rust. Univ. Minn. Agr. Exp. Sta. Tech. Bull. **16**: 1–31. 1923.
8. **Bell, H. P.** Fern rusts of *Abies*. Bot. Gaz. **77**: 1–30. 1924.
9. **Blackman, V. H.** On the fertilization, alternation of generations, and general cytology of the Uredineae. Ann. Bot. **18**: 323–373. 1904.
10. **Buller, A. H. R.** Researches on fungi. III. pp. i–xii, 1–611. London, Longmans, Green and Co. 1924.
11. **Carleton, M. A.** Investigations of rusts. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 63: 1–29. 1904.
12. **Colley, R. H.** Parasitism, morphology and cytology of *Cronartium ribicola*. Jour. Agr. Res. **15**: 619–659. 1918.
13. **Cunningham, G. H.** The rust fungi of New Zealand together with the biology, cytology and therapeutics of the Uredinales. pp. i–xx, 1–261. 1931.
14. **Dietel, P.** Ueber den Pleomorphismus einiger Uredineen. Naturwis. Wochenschr. **4**: 313–314. 1889.
15. ——. Ueber die biologische Bedeutung der Paraphysen in den Uredolagern von Rostpilzen. Hedwigia **41**: 58–61. 1902.
16. ——. Zur umgrenzung der Gattung *Pileolaria* Cast. Ann. Myc. **19**: 300–303. 1921.
17. ——. Riehe Uredinales. In E. & P. Nat. Pfl. **6**: 24–98. 1928.
18. **Dillon Weston, W. A. R.** The effect of ultra-violet radiation on the urediniospores of some physiologic forms of *P. graminis Tritici*. Sci. Agr. **12**: 81–87. 1931.
19. **Fromme, F. D.** Negative heliotropism of urediniospore germ-tubes. Am. Jour. Bot. **2**: 82–85. 1915.
20. **Fukushi, T.** Studies on the apple rust caused by *Gymnosporangium Yamadae* Miyabe. Jour. Coll. Agr. Hokkaido Imp. Univ. **15**: 269–307. 1925.
21. **Grove, W. B.** The British rust fungi (Uredinales), their biology and classification. 412 pp. Cambridge. 1913.
22. **Hart, H.** Factors affecting the development of flax rust, *Melampsora Lini* (Pers.) Lév. Phytopath. **16**: 185–205. 1926.
23. **Hitchcock, A. S.** The genera of grasses of the United States with special reference to the economic species. U. S. Dept. Agr. Bull. 772: 1–307. 1920.
24. **Hutchinson, J.** The families of flowering plants I. Dicotyledons. pp. i–xiv, 1–328. London, Macmillan. 1926.
25. ——. The families of flowering plants. II. Monocotyledons. pp. i–xiii 1–243. London, Macmillan. 1934.
26. **Jackson, H. S.** Present evolutionary tendencies and the origin of life cycles in the Uredinales. Mem. Torrey Club **18**: 1–108. 1931.

27. **Jørstad, Ivar.** Notes on Uredineae. Mag. Naturv. **70**: 325–408. 1932.
28. **Kern, F. D.** The genetic relationship of parasites. Am. Jour. Bot. **2**: 116–131. 1915.
29. **Long, W. H.** Notes on new or rare species of *Ravenelia*. Jour. Myc. **12**: 233–236. 1906.
30. **Miller, Paul R.** Pathogenicity of three red-cedar rusts that occur on apple. Phytopath. **22**: 723–740. 1932.
31. **Moss, E. H.** The uredo stage of the Pucciniastreae. Ann. Bot. **40**: 813–847. 1926.
32. **Newton, Margaret & T. Johnson.** Color mutations in *Puccinia graminis Tritici*. Phytopath. **17**: 711–725. 1927.
33. **Orton, C. R.** A working hypothesis on the origin of rusts, with special reference to the phenomenon of heteroecism. Bot. Gaz. **84**: 113–138. 1927.
34. **Tulasne, L. R.** Second mémoir sur les Urédinées et les Ustilaginées. Ann. Sci. Nat. IV. **2**: 77–196. 1854.
35. **Tulasne, L. R. & C. Tulasne.** Mémoire sur les Ustilaginées comparées aux Urédinées. Ann. Sci. Nat. III. **7**: 12–127. 1847.

CELL RELATIONS IN THE PERITHECIUM OF CERATOSTOMELLA MULTIANNULATA

C. F. Andrus

(with 75 figures)

INTRODUCTION AND HISTORICAL REVIEW

Included in the Ascomycetae are genera in which the asci are developed from isolated free cells, from a fusion of two cells, or within various types of organized fruiting bodies. The latter are commonly distinguished as open (apothecial) or closed (perithecial), although there exist many compound and elaborately constructed variations of the open and closed types of development. The complete history of cell behavior preceding ascus formation is known in a comparatively few species of the apothecial type and in a still smaller number of those in which asci are borne in perithecia. *Ceratostomella multiannulata* Hedgcock and Davidson (**9**) is an especially favorable species for the study of a type of perithecial development first described by Mittmann (**20**) in *C. fimbriata* (E. & H.) Elliott, in which ascus formation is preceded by an extensive multiplication of independent and unwalled cells (fig. 1). A separate paper has been devoted to the structure and development of the ascus in two related species (**2**); in the present communication greater emphasis will be placed on those proliferative stages preceding ascus formation which may be referred to as the development of the ascogenous system.

Since the earliest studies on structure and development in the ascomycetous fungi evidence has existed tending to show that the processes leading to ascus formation in those species with an organized fruiting body may follow fundamentally different courses. The convincing work of Harper and his students led to greater emphasis being directed to that course of development, represented by *Pyronema* and discomycetous species in general, wherein asci are produced following a characteristic crosier device either terminally or laterally on hyphae that are direct outgrowths from an oögonium or group of ascogonial cells. The few recent

investigators in this field who ventured outside the group of discomycetous species have been inclined to interpret their findings in accordance with the above process, even though it were not possible in some cases to follow the various stages intermediate between ascogonium and ascus. This applies in part to the work of Elliott (**11**) and Varitchak (**24**) on *Ceratostomella*,

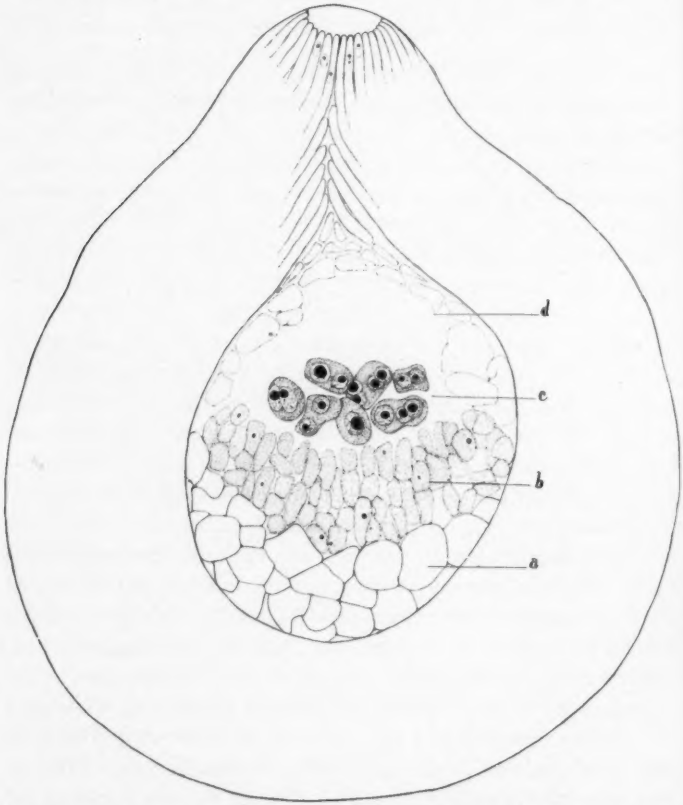


FIG. 1. Diagram showing the interior organization of the perithecium of *Ceratostomella multiannulata* at the beginning of beak formation; *a*, pseudoparenchyma of thin-walled cells; *b*, uninucleate nutritive or space-making cells; *c*, the actively dividing binucleate fertile or ascogenous cells; *d*, a mostly vacant space, but containing disorganized cells at the point where the ostiole will be formed. × 1500.

of Cookson (**8**) on *Melanospora*, and in fact to most of the more recent work on species of so-called Pyrenomycetes. Other investigators, unable to follow the stages intermediate between ascogonium and asci, have concluded that the ascogonium is abortive and that ascogenous hyphae later grow out from purely vegetative cells within the perithecium. A review of early literature in this field has been made by Overton (**23**).

The contribution of Moreau (**21**) concerning *Peckiella lateritia* (Fries) Maire illustrates the tendency of a few investigators to speak of ascogenous hyphae although they are unable to demonstrate the existence of true hyphal growths. Crosiers occur in *P. lateritia*, yet the illustrations shown indicate that each crosier, or each parent cell, is an independent unit free of any hyphal base. Fraser and Chambers (**12**) state that in *Aspergillus herbariorum* Wiggers "the ascogonium becomes septate and each of its cells gives rise to ascogenous hyphae," although their illustrations do not demonstrate clearly the hyphal outgrowths from the ascogonium. The "outgrowths" appear to be single cells that may, either directly or after a crosier type of cell division, develop into asci.

Blackman and Welsford (**5**) described a much-coiled and septate ascogonium in *Polystigma rubrum* D.C. but they considered it to be abortive—ascogenous hyphae developing later from purely vegetative cells within the perithecium. Cayley (**7**) reached much the same conclusion in regard to *Nectria galligena* Bres. McIntosh (**19**) considered the hyphal outgrowths from ascogonia of *Nectria mammoidea* to be abortive structures. He says: "The true ascogenous hyphae arise directly from the vegetative cells at the foot of the cavity. These hyphae consist of a single cell which is generally binucleate."

With respect to some of the above accounts it is pertinent to question whether or not a single cell of the type described can be properly called an ascogenous hypha, and whether the ascogenous cells are true outgrowths or simply fragments resulting from a divison of the oögonium. Questions of this nature are raised especially by what has been learned of cell relations in *Ceratostomella*.

A few investigators have recognized that individual cells of

the ascogonium may become separated and proliferate independently. Brown (**6**) observed such to be the case in *Xylaria tentacularia* B. & Br., and Lupo (**17**) in *Hypoxylon coccineum*. Varitchak (**24**) illustrated a similar condition in *X. polymorpha* (Pers.) Grev. The several independent fragments of the ascogonium proliferate presumably by means of ascogenous hyphae. This type of development would seem to be somewhat intermediate between the discomycetous type and that which is now known to occur in the Ceratostomataceae.

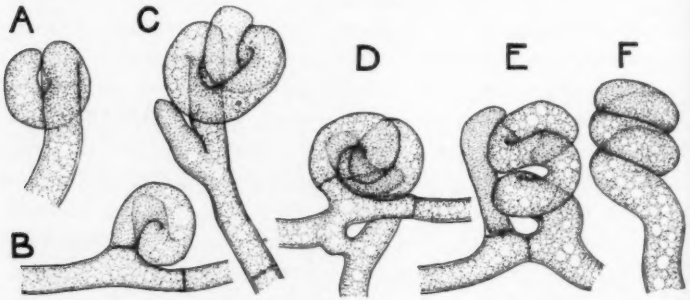


FIG. 2. Perithecial primordia of *Ceratostomella multiannulata* drawn from live material. × 1700.

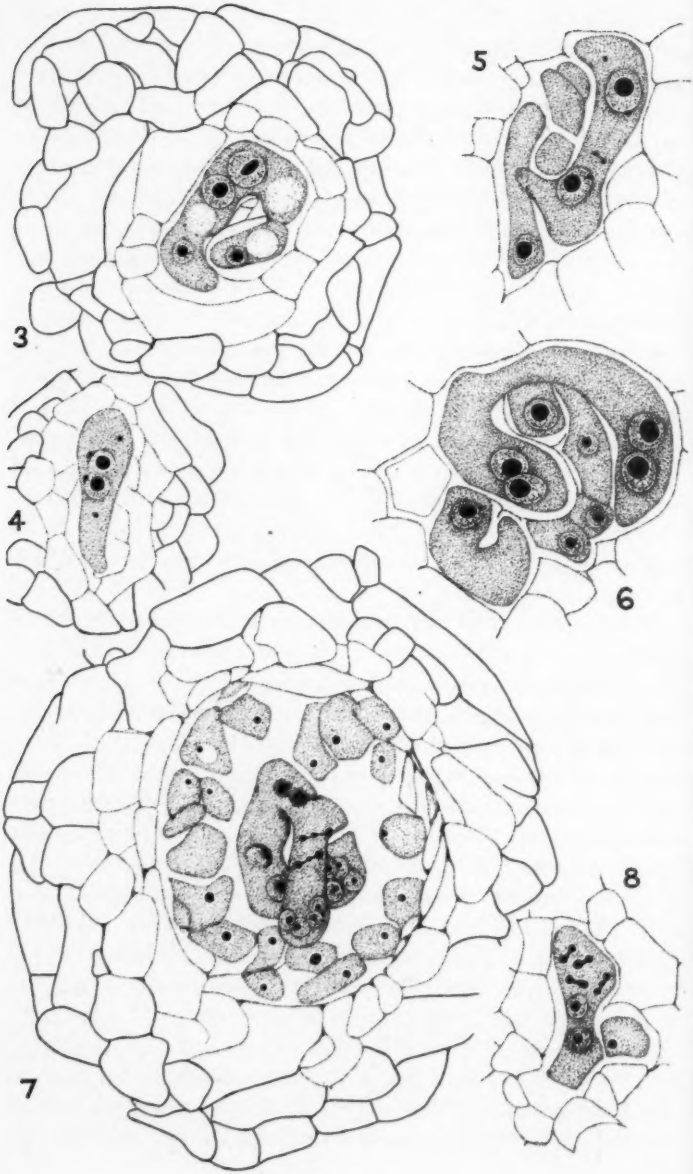
Many of the pioneer observers, having no precedents to guide them, were led to believe that in certain pyrenomycetous species one or more of the ascogonial cells divided repeatedly in three planes in such a manner that a parenchymatous core of cells eventually occupied the interior of the perithecium, and that asci developed from individual cells within the parenchymatous mass. This view was incorporated by De Bary (**10**) in his text on comparative morphology of fungi and is likewise considered with reservations by Gäumann (**13**). Some of the recent texts on structure and development of the fungi, however, ignore opinions of this sort, and in general the work of recent authors lends little credence to the view that multiplication of asci in Pyrenomycetes can result otherwise than as outgrowths from an oögonial cell or group of cells.

Apparently the first to express the belief that a parenchymatous mass of cells resulted from divisions of an oögonium was Kihl-

mann (**16**) who described a central parenchymatic cell mass derived from the division of a single fertile cell of the ascogonium in *Melanospora parasitica* Tul. Mattirolo (**18**) believed that a plectenchymatic group of cells was formed in the young perithecia of *Melanospora stysanophora* Matt. and *M. Gibelliana* Matt. Berlese (**4**), in describing the beginning of perithecium formation in *Melanospora globosa* Berl., concludes that the last cell of the spiral ascogonium divides in three dimensions and that asci appear later from the multiplication of cells thus formed. Nichols (**22**) suggested the possible origin of asci in *Ceratostoma brevirostre* Fuckel (later *Melanospora Zabelli* (Corda) Fuckel) from a central mass of parenchymatous tissue. Bainier (**3**) believed that progressive divisions of the ascogonium in *Melanospora* (*Papulospora*) *aspergilliformis* Eid. resulted in a group of cells from which asci later developed. Each of the above authors either neglected to illustrate the actual formation of a parenchymatous mass of cells from the ascogonium or the illustrations employed were inadequate; nevertheless their opinions were accepted until studies on other genera brought attention to the *Pyronema* type of development.

A fully illustrated paper dealing with the development of perithecia of the *Melanospora* type did not appear until 1917 when Vincens (**25**) published an account of the development of *Melanospora Mangini* and other members of the Hypocreales. According to Vincens the fertile and sterile regions of the ascogonium in *Melanospora* proliferate independently. The fertile portion divides to form a true parenchyma, while the sterile elements ramify in the space between the central parenchymatous mass and the wall of the perithecium. The sterile tissue disintegrates and asci develop within the central core of cells.

In 1928 Cookson (**8**) published a well illustrated account of development in *Melanospora Zamiae* Corda. Without knowledge of Vincens' work, she believed the central core of cells to be hyphal in origin, rather than parenchymatic. The core was thought to become differentiated into fertile and sterile elements, yet she was uncertain whether the two elements had a common or an independent origin. Although unable to trace the origin of the binucleate ascogenous cells, Cookson presumed that they



FIGS. 3–8.

developed from hyphal outgrowths of an enlarged cell of the archicarp. Until some investigator is able to follow the early stages in proliferation of the ascogonium in *Melanospora* the paper by Cookson may be regarded as the most plausible account yet given of development within the genus.

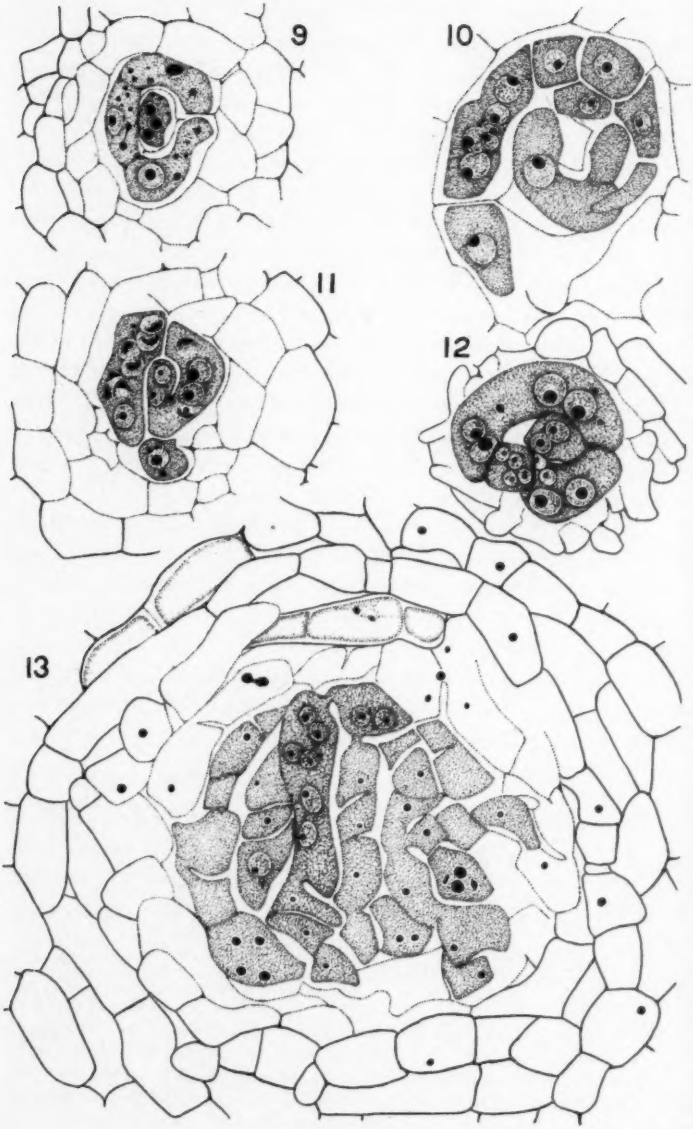
Recent work on the development of *Ceratostomella* by Mittmann (**20**) and by Andrus and Harter (**1**) (**2**) renders the facts in the case of *Melanospora* susceptible to a new interpretation. *C. multiannulata* especially, to be described below, seems to conform very closely with the published accounts of development in *Melanospora*. Yet it has been necessary to conclude on the one hand that no true parenchyma is formed by divisions of the ascogonial cells, and, on the other, that asci do not arise as true hyphal outgrowths from a fertile cell of the ascogonium. These conclusions are made possible by a detailed study of cell relations and the divisions of individual cellular units during the proliferative period leading up to ascus formation.

The writer is indebted to Dr. W. W. Diehl, Division of Mycology and Disease Survey, the U. S. Department of Agriculture, and Dr. R. F. Griggs, Professor of Botany, George Washington University, for valuable criticism during the course of the investigation, and to Dr. L. L. Harter, Division of Fruit and Vegetable Crops and Diseases, U. S. Department of Agriculture, who has encouraged a continuation of work in this field and who has assisted in the preparation of the manuscript.

METHODS

Ceratostomella multiannulata was isolated from lumber by R. W. Davidson, of the Division of Forest Pathology, U. S. Department of Agriculture, who supplied the writer with fixed material and with live cultures from which additional preparations were made. Fixations were made on the 6th day of growth on Thaxter agar. The habit of growth is such that perithecia in many stages of

FIGS. 3–8. 3, a young perithecium showing the first division of the ascogonium into a central binucleate cell and terminal uninucleate cells; 4, the primary binucleate cell in a young perithecium; 5, an early stage in linear growth of the binucleate ascogonium; 6, linear growth of the fertile portion of the ascogonium; 7, the coiled fertile portion of the ascogonium previous to fragmentation, surrounded by uninucleate space-making cells; 8, multiplication of nuclei in the fertile portion of the ascogonium. × 2700.



FIGS. 9–13.

development can be obtained in the same section. The earliest stages in development were also studied in live mounts.

Material for sectioning was fixed in either Bouin's solution or Flemming's strong solution diluted with an equal part of water. The agar blocks were imbedded in commercial parawax and sectioned 4 to 6 μ in thickness. Either fixative followed by haematoxylin gave superior results in demonstrating the early proliferation of the ascogonium. The triple combination (safranin, gentian-violet and orange G) was also tried but seemed generally inadequate. No combination has given entirely satisfactory delineation of nuclear structure in the ascus.

ORIGIN OF THE ASCOGONIUM

According to the evidence from the behavior of single spore strains a bisexual condition exists in *Ceratostomella multiannulata*. Davidson (unpublished) has observed that fertile perithecia are not produced in cultures derived from single ascospores or from single conidia, but that perithecia form abundantly where certain pairs of single spore isolates are grown in combination. The two kinds of sexually differentiated thalli appear to be approximately equal in number. There are slight differences in the appearance of cultures of the two sexes but apparently no very definite morphological characters by which they can be identified. Ascogonial coils, or rudimentary perithecia, are produced by cultures of both sexes, and where the two grow in contact on agar media two rows of perithecia are sometimes formed separated by a space of 2 to 3 millimeters. It is probable, therefore, that a reciprocal migration of nuclei occurs at the time of fertilization. The actual mechanism of fertilization will not be developed here but has been made the subject of a separate investigation.

The primary coil of the perithecium (FIG. 2), of which the terminal portion later becomes the ascogonium, may attain the proportions of the helicon frequently described for members of

FIGS. 9–13. 9, linear growth of uninucleate elements of the ascogonium with a fertile (trinucleate) cell in the center; 10, origin of the uninucleate space-making cells; 11, fragmentation of the fertile portion of the ascogonium; 12, a stage in fragmentation of the coiled fertile portion of the ascogonium; an adjacent section shows uninucleate space-making cells; 13, a stage in fragmentation of the ascogonium. × 2700.

the Aspergillaceae (**13**). An antheridium, generally similar to that described in *Ceratostomella fimbriata* (**1**) and *C. moniliformis* (**2**), appears to be present in at least some instances (FIG. 2*C*, *E*) but the question of how fertilization occurs will be disregarded at this time. The binucleate condition in the ascogonium has usually appeared by the time the first layers of enveloping hyphae are in place. The first division of the ascogonium is brought about by a simultaneous cleavage at two points, giving origin to terminal and basal uninucleate cells and a subterminal binucleate cell (FIG. 3). Figure 4, owing to the size of the perithecium is regarded as a stage previous to the first division.

The binucleate and uninucleate elements resulting from the first division of the ascogonium continue to develop independently. The original hyphal wall, still partially visible at the early stage shown in figure 3, later becomes completely dissolved and the cells occupying the perithecial cavity are essentially naked protoplasts. Proliferation of the binucleate or fertile cell at first consists of an extended linear growth (FIG. 5, 6, 75*B*), which, due to the limitations of the small perithecial cavity, is in the form of an irregular coil (FIG. 7, 11, 12, 75*A*). Linear cell growth is accompanied by rapidly recurring conjugate nuclear divisions (FIG. 7, 8). Although a well developed ascogonial coil is a multinucleate structure the nuclei are conspicuously arranged in groups of 2 or 4.

Ordinarily fragmentation of the fertile body does not begin to occur until the 8-nucleate stage is attained. In the meantime the uninucleate or sterile elements of the original ascogonium have undergone an independent proliferation in the region between the fertile coil and the margin of the perithecial cavity (FIG. 9, 10). Early growth of the uninucleate cells is likewise linear but the hyphal units later break up into numerous uninucleate cells that arrange themselves on the periphery of the cavity and surround the fertile coil (FIG. 7).

At approximately the stage shown in figure 7, the multinucleate fertile coil begins to fragment into independent units each possessing two or more nuclei. The appearance of the bodies undergoing division may suggest superficially the occurrence of division in 3 planes (FIG. 13), or the cleavage of a multinucleate

body into a parenchymatous mass of cells, such as was believed by some of the earlier observers to occur in species of *Melanospora*. This is evidently not the case since the dividing cells do retain a fundamentally linear relation to each other even though protoplasmic connections may be severed.

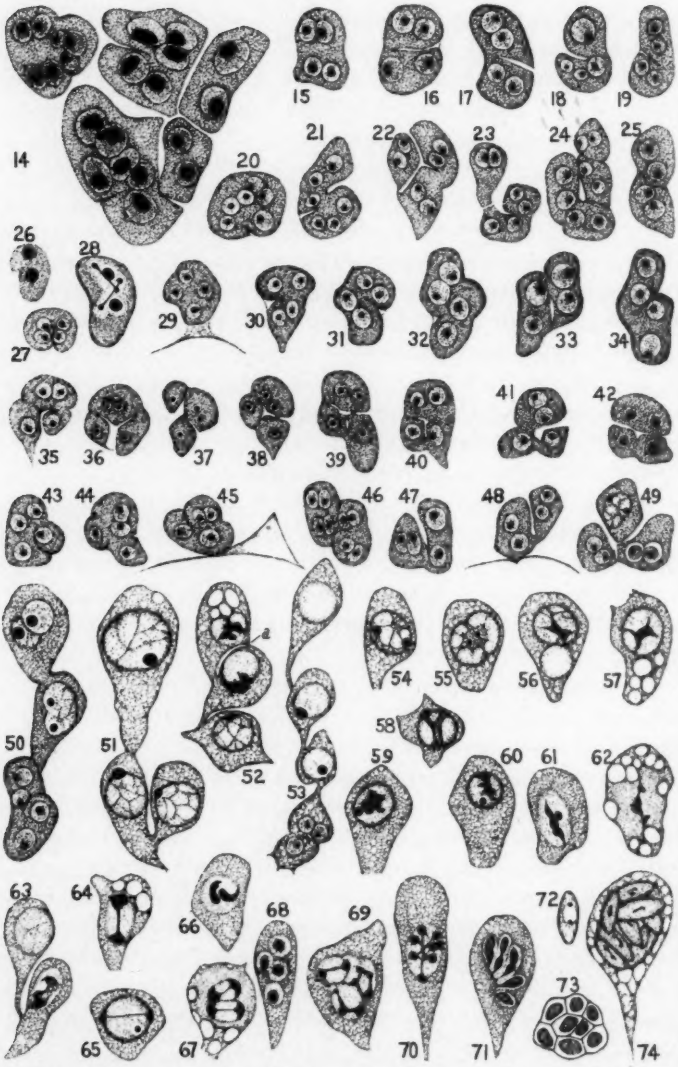
MULTIPLICATION OF ASCOGENOUS CELLS

An early and a late phase in the proliferation of ascogenous cells are conspicuous in *Ceratostomella multiannulata*. The transition from the early to the late phase of development is marked by a characteristic change in the organization of the perithecium. The early phase of cell proliferation begins with the fragmentation of the fertile multinucleate coil described above. Each fragment of the divided ascogonium continues to grow and divide independently. Eventually a multitude of the individual 2- or 4-nucleate cells occupy the perithecial cavity.

During the early divisions of the fertile cells there occur changes in the arrangement of the sterile or uninucleate elements. The uninucleate cells, which formerly surrounded the fertile coil on all sides (FIG. 7), withdraw from or become disorganized on the side of the cavity where the future beak or neck of the perithecium is to be formed.

At the beginning of beak formation, the perithecium is constructed as indicated in figures 1 and 75*C*. The fruiting body at that stage is composed of an outer pseudoparenchymatous region of thick-walled pigmented cells with an apical beak, and an inner region constructed of four layers: 1, a basal parenchyma of thin-walled, swollen and sterile cells; 2, a compact, crudely palisade layer of uninucleate cells, still undergoing some proliferation; 3, the fertile layer of loosely arranged independent ascogenous cells, containing two or more nuclei each; 4, a mostly vacant space, containing disorganized cells at the point where the ostiole will appear. The beak later becomes enormously elongated, and the interior of the fruiting body becomes altered in appearance.

At the beginning of the later phase in the proliferation of ascogenous cells, the uninucleate elements have ceased their development and become disorganized, so that the fertile cells,



FIGS. 14–74. 14, a group of ascogenous cells from a young perithecium, showing the larger size of individual protoplasts and nuclei during the early phase of cell multiplication; 15–21, stages in simple unilateral cleavage during a later period of cell multiplication in the perithecium; 22–25, cell linkage; 26, an

or the future asci, come to rest directly upon the parenchyma of thin-walled cells at the base of the perithecial cavity. This later stage is represented in figure 75*D*. Although the disappearance of the uninucleate elements at this time may suggest that they have functioned as space-making cells it does not appear that the latter function is a necessary one, since in *Ceratostomella fimbriata* (1) the space-making seems to proceed without any proliferation of uninucleate elements. Yet it is perhaps true that the uninucleate independent cells that undergo a limited development in perithecia of *C. multiannulata* correspond in certain respects to the paraphyses in discomycetous species.

A more important feature of the later phase in the proliferation of ascogenous cells is the appearance of the crosier type of cell division. There are few figures showing nuclear division at this stage in *Ceratostomella multiannulata* yet the conformation and linkage of dividing cells, together with the position of nuclei, demonstrate that crosier divisions as well as simple cleavages occur in this species (FIG. 15–49) as well as in *C. moniliformis* and *C. fimbriata* (2).

Changes in cell shape play an important role during cell

early stage in crosier formation; 27, a stage in cleavage that may result in a direct or an indirect cell division; 28, a stage in nuclear division in a crosier; 29, an ascogenous cell in close contact with a sterile parenchymatic cell at the base of the perithecial cavity; 30–34, all appear to be stages in direct or unilateral cell cleavage and emphasize changes in cell shape (a persistent surface membrane is frequently observed at points of cleavage); 35–37, the 3-cell stage in crosier formation; 38–42, stages in fusion of uninucleate portions of the crosier; 43–45, an indirect cell division that appears to be intermediate between crosier formation and a process of budding (contact with disorganized walls of the sterile parenchyma is indicated in figure 45); 46, change in cell shape accompanying incomplete cleavage of a 4-nucleate ascogenous cell; 45–53, linkage of ascogenous cells and young asci (cleavage does not appear to have been completed at *a*, of fig. 52); 54, 55, nuclear fusion at the beginning of ascus formation; 56–59, first nuclear division in the ascus, showing the gathering or condensation of chromatic material; 60–62, first nuclear division, showing the characteristic 4-lobed chromatin mass at metaphase and early anaphase; 63–65, anaphase of the first nuclear division; 66–68, stages in the second nuclear division in the ascus; 69, a stage in the third nuclear division in the ascus; 70, a young ascus with the 8 nuclei arranged in a crude circle and joined together by strands of protoplasm; 71, a young ascus with spore rudiments radiating from a common lateral base; 72, a nearly mature ascospore, showing two chromatic centers in a single nucleus; 73, a cross section of a mature ascus; 74, a nearly mature ascus. × 2700.

division. Having observed the various intermediate steps (FIG. 30–33) one can easily visualize the gliding motions that must occur while such a structure as that represented in figure 29 assumes the appearance shown in figures 34 and 50. By means of change of shape alone, a 4-nucleate "crosier" of the type shown in figure 43 may contrive to have joined two distal uninucleate points without need of fusion; which is equivalent to saying that two terminal points of such a crosier may fuse completely without their ever having been entirely separated.

In the processes of division and changes in cell shape and cell linkage evidence can be found for the presence of a protoplasmic surface membrane (FIG. 30–32, 36) enclosing the otherwise apparently naked cells. The slender protoplasmic strands which sometimes provide a continuity between asci (FIG. 38, 39, 52) may be constructed wholly of the more tangible surface film present on the naked protoplasts, but it seems more probable that connecting filaments of the type shown are strands of cytoplasm corresponding to the plasmodesma that may be observed in a series of walled cells.

The crude chains of cells illustrated in figures 49–53, and similar linked groups described in *Ceratostomella moniliformis* and *C. fimbriata* (1) (2), comprise the only suggestion of ascogenous hyphae observed in the genus. It is important to emphasize that they represent independent groups of cells and not merely parts of a continuous hyphal network such as is to be observed in discomycetous species. Linkages of the kind illustrated are not found among the freely dividing cells that result from the first fragmentation of the ascogonium (FIG. 14) and the fact suggests the interpretation that each one of the multitude of independent cells resulting from the early proliferative stage is equivalent to a separate ascogonium and that each such ascogonium gives rise to an independent group of asci. Such an interpretation seems to offer no advantage over the view that independent cell proliferation in perithecia of *Ceratostomella* corresponds to the proliferation of ascogenous hyphae in discomycetous species.

NUCLEAR BEHAVIOR IN THE ASCUS

Individual asci of *Ceratostomella multiannulata* are smaller than in any related species investigated and also they have been difficult to stain. Stages in nuclear fusion in the ascus are observed frequently (FIG. 54, 55) but they reveal no new details concerning the process. The fusion nucleus is perhaps exceptionally large in proportion to cell size; while the nucleolus is proportionately small. The stainable contents of the nucleus consist of a few faint strands that often extend the entire breadth of the nuclear vesicle (FIG. 51, 52). An appearance such as illustrated in figure 58 seems to precede the first nuclear division.

First division stages are shown in figures 56 to 65. The nucleolus often persists during the first division but not thereafter. There appear to be no more than four discrete bodies of chromatin distributed along the crude spindle (FIG. 59–62); a single 2 to 4-lobed mass is commonly observed. Two chromatin bodies, or a single compound body, appear to move to each pole (FIG. 63). Near the close of the first division single masses of chromatin are observed on opposite faces of the original nuclear vesicle and are connected by a single slender filament (FIG. 64, 65).

The beginning of the second nuclear division seems to be indicated by such an appearance as that shown in figure 66. Later the two spindles appear to occupy separate hyalospheres (FIG. 67) and the original nuclear vesicle is no longer visible. The few intermediate stages seem to indicate that no reduction in the amount of chromatin or in number of chromatin bodies occurs during the second nuclear division.

During the third nuclear division the four advanced spindles (FIG. 69) appear to occupy separate hyalospheres. There is a reduction in the amount of chromatin but it would be presumptive to state that there is a reduction in number of chromosomes. An inner vesicle such as usually appeared at approximately the 4-nucleate stage in *Ceratostomella moniliformis* and *C. fimbriata* (2) has not been observed in *C. multiannulata*.

MATURATION OF ASCI

A cleavage of the cytoplasm surrounding the inner spore-producing region in *Ceratostomella moniliformis* (2), and the

presence of an endogenous wall in *C. fimbriata* (1) (2), in a position corresponding to the cleavage in *C. moniliformis*, were conspicuous features of advanced stages in ascus formation in those two species and were regarded as evidence of the vesicular nature of the spore-producing central region of the ascus. The non-appearance of such a vesicle in *C. multiannulata* is perhaps the one point in which ascus formation differs fundamentally from the two species mentioned above.

Although there appears to be no true ascus wall, the peripheral layer, like the intervacuolar layers, is more substantial and remains entire up to the time of spore wall formation (FIG. 74). The process of spore delimitation has not been followed in detail yet it evidently follows a course similar to that observed in *C. moniliformis* and *C. fimbriata* (2), except that the spore-producing region does not appear to be vesiculate at any stage. The eight nuclei become arranged in a crude circle, with filaments of an unidentified nature connecting them all to a common point or base (FIG. 70). Later the young spores appear to be attached to a common base (FIG. 71) which is usually lateral to the long axis. Figure 73 is a cross-section and figure 74 a longitudinal section of nearly mature asci. The spore walls seem to originate from the cytoplasmic layer at the margin of each spore vesicle. A membranous attachment, such as was observed in *C. moniliformis* and *C. fimbriata* (2) has not been observed on ascospores (FIG. 72) of *C. multiannulata*.

DISCUSSION

It is probable that the most important fact brought out in the recent investigations on *Ceratostomella* concerns a fundamental character possessed in common by several species, namely, the independent proliferation of ascogenous cells following fragmentation of the ascogonium. It is believed that the type of cell proliferation preceding ascus formation demonstrated to occur, first by Mittmann (20) and later by Andrus and Harter (1) (2), and in the present account, represents a fundamentally different course of development from that which occurs in species of Discomycetes as represented by the lichen fungi and *Pyronema* (15). In discomycetous species a multiplication of asci follows

direct hyphal outgrowths from an ascogonium. In the group of Pyrenomycetes represented by *Ceratostomella* the ascogonium divides into numerous independent binucleate cells each of which continues to divide independently.

Intermediate between the type of cell proliferation that proceeds from the ascogonium in Discomycetes and the type that occurs in *Ceratostomella* may be found that occurring in such species as *Xylaria tentacularia* (**6**) and *Hypoxylon coccineum* (**17**) in which the ascogonium becomes separated into several independent portions, each of which presumably gives origin to a system of ascogenous hyphae. Other types of development are represented by those groups, such as the mildews and the Laboulbeniales, in which a single ascus or a comparatively few asci are produced in a perithecium. In certain species the oögonium or single-celled ascogonium would appear to be transformed directly into a single ascus. In others the ascogonium apparently divides into two or more portions which develop directly into asci. In still other species the asci originate as single-celled outgrowths from the ascogonium, in which case they have been called ascogenous hyphae (**12**) (**21**). Considering all of the above types of development there is reason to look upon the originally single-celled ascogonium or oögonium as a potential ascus, which may develop into a single ascus or may undergo various types of proliferation that lead to a multiplication of asci. The differences between the various types of proliferation, however, may be important ones and conceivably may have great taxonomic value.

It is notably the case that, previous to the work of Mittmann (**20**) and of Andrus and Harter (**1**) on *Ceratostomella fimbriata*, all attempts to describe a system of independent cell divisions preceding ascus formation were met with skepticism. The views expressed by the above writers also have been rejected by Gwynne-Vaughan and Williamson (**14**), and may continue to be regarded doubtfully by those who presumably have not had occasion to examine the species. Previously Andrus and Harter (**1**) introduced a discussion of publications concerning the genus *Monascus*. Early in the present account numerous references are made to investigations in the genus *Melanospora*. In respect to both genera there has been controversy over the question of

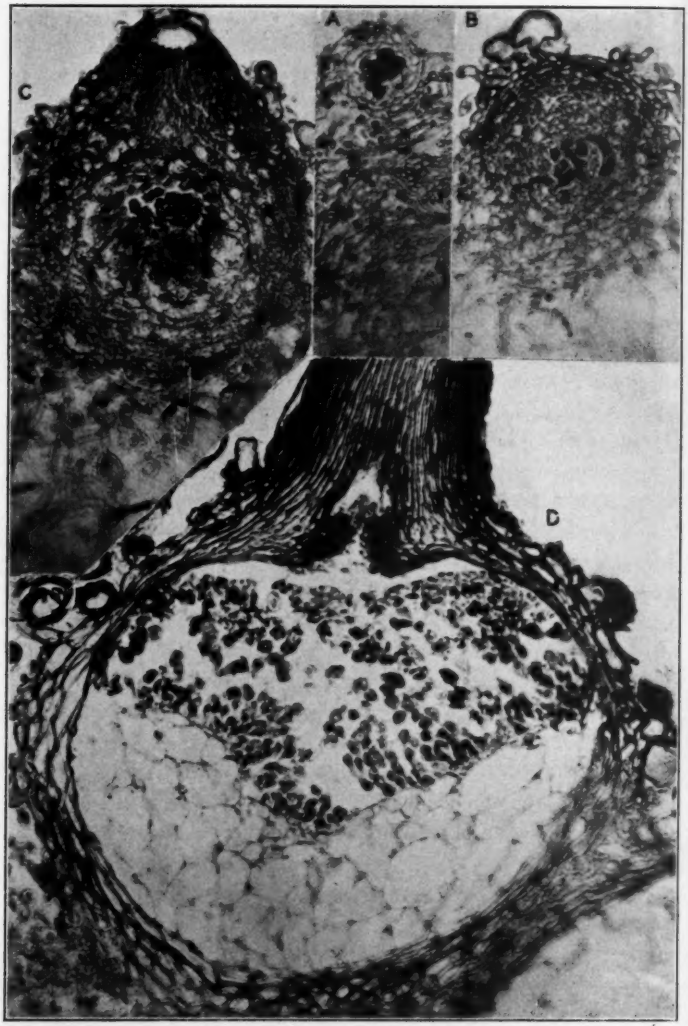


FIG. 75. *Ceratostomella multiannulata.* A, photomicrograph of a young perithecium, showing an early appearance of the coiled and deeply stained ascogonium, × 600; B, photomicrograph of a young perithecium, showing the first divisions of the ascogonium into uninucleate and binucleate cells, × 600; C, photomicrograph of a stage at the beginning of beak formation, showing the binucleate fertile cells surrounded by uninucleate "space-making" cells, × 600; D, a mature perithecium with crude chains of asci in direct contact with the sterile pseudoparenchyma at the base of the cavity, × 500.

whether the first proliferation of the ascogonium led to the formation of a true parenchyma in the perithecial cavity or whether the proliferation was in the form of hyphal growths.

In the present investigation it has been possible to supply some of those missing details that led previously to uncertainty regarding the early proliferative stages in the perithecia of *Melanospora*. *Ceratostomella multiannulata* has proved to be favorable material for a detailed study of the early fragmentation of the ascogonium and the later divisions of the independent ascogenous cells. It is believed that the processes of cell multiplication, fully described and illustrated above, require no further discussion. It should be repeated, however, that the facts do not support the often expressed belief that asci may arise from a parenchymatous mass of cells within the perithecium. On the other hand they demonstrate that the first proliferation of the ascogonium need not be in the form of hyphal outgrowths.

SUMMARY

The development of the ascogenous system in the perithecium of *Ceratostomella multiannulata* follows the fragmentation of an originally binucleate unwalled ascogonium. The first division of the ascogonium is indirect and results in the formation of two uninucleate fragments and a single binucleate cell. The binucleate or fertile portion of the ascogonium undergoes a linear growth accompanied by conjugate nuclear divisions. At approximately the 8-nucleate stage, the fertile coil divides into independent units of 2 or 4 nuclei each. Each unit continues to divide independently. The uninucleate fragments resulting from the first division of the ascogonium undergo an independent proliferation within the perithecial cavity and give origin to a layer of space-making cells that at one stage surrounds the group of binucleate protoplasts. The uninucleate or space-making cells later collect at the base of the perithecial cavity where they dwindle in number and disappear before the perithecium reaches maturity.

Successive divisions of the binucleate fragments of the ascogonium result in the formation of a multitude of minute, independent and unwalled cells that later develop into asci. Stages

in division of the ascogenous cells include the crosier as well as several other, both direct and indirect, types of cell cleavage. Cell divisions are accompanied by significant changes in cell shape. Short chains or independent groups of cells constitute the only suggestions of hyphal growths to be observed in the perithecium. Developing asci are frequently linked together in short series, while actively dividing cells are mostly unattached.

Actively dividing cells in an advanced perithecium cover the lower face of the perithecial cavity and appear to consume the pseudoparenchyma of thin-walled cells lining the interior. The "space-making" function, therefore, does not appear to be restricted to the system of uninucleate cells that is present in the perithecium at an early stage of development.

The asci are unwalled. Ascospore formation is restricted to a central region of the ascus cytoplasm which, however, is not clearly vesiculate. Immature ascospores appear to be attached at a common base which is usually lateral to the longer dimension of the ascus. Deliquescence of the ascus involves a dissolution of the peripheral layer of cytoplasm and a separation of the closely compact group of 8 spores.

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LITERATURE CITED

1. **Andrus, C. F. & L. L. Harter.** 1933. Morphology of reproduction in *Ceratostomella fimbriata*. Jour. Agr. Res. **46**: 1059–1078.
2. ——, ——. Organization of the unwalled ascus in two species of *Ceratostomella*. (In press.)
3. **Bainier, G.** 1907. Evolution du *Papulospora aspergilliformis* et de deux *Ascodesmis* nouveaux. Bull. Soc. Myc. Fr. **23**: 132–140.
4. **Berlese, A.** 1892. Intorno allo sviluppo di due novi Ipocreacei. Ricerche micobiologichi. Malpighia **5**: 386.
5. **Blackman, V. H. & E. J. Welsford.** 1912. The development of the perithecium of *Polystigma rubrum*. Ann. Bot. **26**: 761–767.
6. **Brown, H. B.** 1913. Studies in the development of *Xylaria*. Ann. Myc. **11**: 1–13.
7. **Cayley, D. M.** 1921. Some observations on the life history of *Nectria galligena*. Ann. Bot. **35**: 79–92.
8. **Cookson, I.** 1928. The structure and development of the perithecium in *Melanospora Zamiae*, Corda. Ann. Bot. **42**: 255–269.
9. **Davidson, R. W.** Fungi causing stain in logs and lumber in the Southern States, including five new species. Jour. Agr. Res. (in press).

10. **De Bary, A.** 1887. Comparative morphology and biology of the fungi, mycetozoa and bacteria. Authorized English Transl. by H. E. F. Garnsey, rev. by I. B. Balfour. 525 p. illus. Oxford.
11. **Elliott, J. A.** 1925. A cytological study of *Ceratostomella fimbriata* (E. & H.) Elliott. Phytopath. **15**: 417–422.
12. **Fraser, H. C. I. & H. S. Chambers.** 1907. The morphology of *Aspergillus herbariorum*. Ann. Myc. **5**: 419–431.
13. **Gäumann, E. A.** 1928. Comparative morphology of fungi. (Transl. C. W. Dodge.) 701 p., illus. New York and London.
14. **Gwynne-Vaughan, H. C. I. & H. S. Williamson.** 1934. The cytology and development of *Ascophanus Aurora*. Ann. Bot. **48**: 261–272.
15. **Harper, R. A.** 1900. Sexual reproduction in *Pyronema confluens*, and the morphology of the ascocarp. Ann. Bot. **14**: 321–400.
16. **Kihlmann, O.** 1885. Zur Entwickelungsgeschichte der Ascomyceten. Acta. Soc. Sci. Fenn. **14**: [309]–351.
17. **Lupo, P.** 1922. Stroma and formation of perithecia in *Hypoxylon*. Bot. Gaz. **73**: 486–495.
18. **Mattirolo, C.** 1886. Sullo sviluppo di due nuovi Hypocreacei e sulle sporebulbilli degli Ascomyceti. Nuovo Giorn. Bot. Ital. **18**: 121.
19. **McIntosh, A. E. S.** 1927. Perithecial development in *Nectria mammoidea*. Rep. Brit. Assn. Adv. Sci. **95**: 387–388.
20. **Mittmann, G.** 1932. Kulturversuche mit Einsporstämmen und zytologische Untersuchungen in der Gattung *Ceratostomella*. Jahrb. Wiss. Bot. **77**: 185–219.
21. **Moreau, F.** 1914. Sur le Developpment du Périthèce chez une Hypocréale, le *Peckiella lateritia* (Fries) Maire. Bull. Soc. Bot. Fr. **61**: 160–164.
22. **Nichols, M. A.** 1896. The morphology and development of certain Pyrenomycetous fungi. Bot. Gaz. **22**: 301–327.
23. **Overton, J. B.** 1906. The morphology of the ascocarp and spore-formation in the many-spored asci of *Thecotheus Pelletieri* I. Bot. Gaz. **42**: 450–489.
24. **Varitchak, B.** 1931. Contribution a L'etude du developpment des Ascomycetes. Le Botaniste **23**: 1–142.
25. **Vincens, F.** 1917. Recherches organogéniques sur quelques Hypocréales. Thesis (a la Faculté des Sciences de Paris) Lons le Saunier. 170 p. illus.

NORTH AMERICAN POLYPORES—I. POLYPORUS SQUAMOSUS AND ITS VARIETIES

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There seems to be considerable uncertainty with regard to the distribution and prevalence of *Polyporus squamosus* (Huds.) Fries, within its North American habitat. Nor has there been any clear recognition of its varieties, either here or abroad. It has been said that this species is of common occurrence in the United States, but it has been more generally reported as rare. American distribution has been limited by some to the Northeastern States, though it has been collected in Ontario, Manitoba, Kansas and Colorado, and the present report extends its range to western Montana. The fungus is said to be found attacking only deciduous trees, and to produce mature pilei that are typically from 5 to 40 cm., wide. But in Minnesota, it has been intimated, *P. squamosus* grows on the ground where it is said to attain a width of 7 feet [210 cm.] and a weight of 40 pounds. All of which shows just how uncertain our information is with regard to the habits of this polypore.

Polyporus squamosus has always been considered, by both European and American mycologists, to be a species based upon *Boletus squamosus* as described by Hudson. They have failed to recognize the fact that it was Micheli (**1729**) and not Hudson (**1778**) who first described this fungus under its generally accepted specific name. It is true that Hudson did give a brief description of this species in his "Flora Anglica." I can find no intimation, however, that he considered it a new species. Micheli described this fungus as *Agaricum squamosum*, and forty-nine years later Hudson transferred it to the genus *Boletus* in order to bring it into conformity with his more advanced scheme of classification. In doing this Hudson made no claim to the discovery of a new species. This fact is irrefutable for he includes a brief synonymy. He fails to tell us, however, why he gave preference to Micheli's name instead of using that proposed by Sterbeck (**1675**), though

Auricula flammea of this earlier writer is among his synonyms. It is evident that, from an historical viewpoint, Hudson's description has no more significance than one appearing in any local descriptive flora. And yet, because of nomenclatorial idiosyncrasies, followers of the International Code must give Hudson all the credit, and relegate any citation of Micheli's original name to a place among synonyms.

The "North American Flora" (Murrill **1908**) includes this species under the name *Polyporus caudicinus*. Murrill (**1903**) recognized the fact that *Boletus caudicinus* of Scopoli (**1772**) antedated *Boletus squamosus* as published by Hudson, but failed to trace the original source of Hudson's name. On this basis he changed the name of the fungus to *Polyporus caudicinus* (Scop.) Murr. While doing this Murrill also failed to recognize the fact that this same fungus had been described by Sterbeck (**1675**) as *Auricula flammea*, by Dillenius (**1718**) as *Agaricus villosus*, by Schaeffer (**1763**) as *Boletus Juglandis* and by Haller (**1768**) as *Polyporus sessilis* before Scopoli's publication appeared. He should have used the name *Polyporus flammeus* had he wished to set aside the International Code and abide by strict priority. The following year Murrill (**1904**) does include *Boletus Juglandis* Schaeff., as a synonym, but gives Schaeffer's date of publication as 1774 instead of 1763, thus through an error saving his combination.

In spite of its prevalence, occasional errors of identity and misinterpretations have crept into the literature. We find that at times *Polyporus giganteus* (Pers.) Fries, has been considered synonymous with *P. squamosus*. The cause of this error can possibly be traced to Harzer (**1845**), who described and very clearly figured the latter species under the former name. *P. giganteus* and *Boletus acanthoides* of Bulliard (**1790**) are equivalent, and very different from *P. squamosus*.

Boletus elegans of Bolton (**1789**, PL. 76) has appeared at times as a synonym of both *Polyporus giganteus* and *P. squamosus*. Obviously this species of Bolton's cannot be a synonym of both of these polypores. It clearly belongs among the numerous synonyms of *P. giganteus*. In this connection one must not confuse *B. elegans* Bolt., with *B. elegans* Bull., two very different fungi.

Polyporus squamosus is clearly distinct and recognizable from other members of the genus *Polyporus* with large favoloid pores. The species has a long history, and the distinction of being one of the first members of the polyporoid group to have been illustrated in a clearly recognizable manner. Clusius (**1601**) has given us, in his work on Hungarian fungi, a woodcut so well executed as to make perfectly clear the fungus he intended to portray. Sterbeck (**1675**) was the next to clearly illustrate this plant. In his "Theatrum Fungorum" there are two copper-plate engravings, both of which represent *P. squamosus* in an unmistakable manner. With the numerous illustrations and descriptions that have subsequently appeared there would seem to be little reason why the species should not be readily recognized, and yet its boundaries and limitations have been variously defined.

In Europe, *Polyporus squamosus* is one of the most common causes of timber decay among a wide variety of living deciduous trees. It is said to attack those of the forest, park or garden indiscriminately. The only exception to its partiality for deciduous trees has been noted in England where the fungus has been reported parasitic on yew.

The situation in North America is apparently quite different from that in Europe. Though found occasionally in the region from West Virginia, Missouri, Kansas and Colorado northward, and east of the Rocky Mountains, collections are rare and published reports are based upon few specimens.

Murrill (**1904**, **1908**) reports the species as collected in Ontario by Dearness, in Connecticut by Underwood and New York by himself. White (**1905**) reports two collections from Connecticut, one from the vicinity of East Hartford and the other from Tolland County. In none of these cases is the host mentioned, and both specimens are missing from the White collection at the Connecticut State College.

Peck (**1875**) cites a collection found growing upon the trunk of an elm at Albany, New York. More recently Lowe (**1934**) reports its presence in New York state upon the American elm and black willow. McIlvaine (**1900**) adds Massachusetts with material collected by Sprague, Iowa by Macbride, and West

Virginia, New Jersey and Pennsylvania by himself, but without further mention of host than "fallen trunks and on stumps." His opinion is that the species is rare in America. McIlvaine's plate (PL. 130) would seem to approach the form described as *Polyporus fagicola* Murr., though somewhat larger and possessing a dark based stipe. Overholts (**1933**) also reports the species from Pennsylvania, and as growing from wounds in living deciduous trees and rare.

Apparently Pennsylvania and West Virginia are as far south as *Polyporus squamosus* has been reported along the Atlantic seaboard. Passing to the westward one finds it mentioned first by Cragin (**1884**) from near Topeka, Kansas, and later by Overholds (**1914, 1915**), who says it is rare in the states of Ohio, Minnesota, Missouri and Kansas. Overholts, unfortunately, only limits his hosts as living deciduous trees. At the same time Neuman (**1914**) reports a collection made in Madison, Wisconsin, but gives no host and declares the fungus to be rare. Dodge (**1914**) reports gathering one centrally stiped plant at Algona, Wisconsin, on maple. Kauffman (**1917**) desiring, as he says, to put on record data of many years concerning the distribution of Basidiomycetes in Michigan, published an index in which he reports *P. squamosus* on elm and willow.

The most westerly collection reported is that of Shope (**1931**), who found the species growing upon *Populus* spp., in the plains zone of Colorado. To the northward Bisby, Buller and Dearness (**1929**) report "*Polyporus squamosus* Pers.," as rare and seen but twice in the vicinity of Winnipeg, Manitoba. Presumably this reference is to our species, though the authorship of the fungus is delegated to Persoon who, while he gave this particular fungus three new names, did not make use of this one.

There are, in the herbarium of The New York Botanical Garden, two apparently unreported collections that are of importance in extending the range of our fungus. A collection made by Lansing, in Jackson Park, Chicago, from the base of a cottonwood tree adds the state of Illinois to our list. No other data accompany this collection. The second is an excellent specimen gathered by Dr. H. D. House, May 26, 1911, from a dead log of *Aesculus octandra* Marsh, at Sunburst, Haywood

County, North Carolina, at an altitude of 3,200 feet. This is of importance as showing that the distribution may extend southward in the Appalachian Mountains, and in adding a new host. A third collection, one made by Ellsworth Bethel in Colorado, is also worthy of note, though without further data, as seconding Shope's report from that western state.

Personally I have collected *Polyporus squamosus* but three times. The first collection was made on the western slope of the Mission Mountains, in the vicinity of Yellow Bay, Flathead Lake, Montana, at approximately 3,500 feet elevation, July 23, 1918, on living *Populus trichocarpa* T. & G. The second was found in the vicinity of Bigfork, at the northern end of Flathead Lake and 3,000 feet elevation, July 7, 1921, growing from the base of an over mature *Acer glabrum* Torr. Both of these collections were deposited in the herbarium of the University of Montana Biological Station, Yellow Bay, Montana. While these hosts are of some interest, the chief interest in these collections lies in the fact that they were made in a locality west of the Continental Divide. Because of this they must be considered, at least for the present, as sporadic occurrences, though it may be admitted that the Northwest has been explored but comparatively little by mycologists.

My third collection was made at Storrs, Tolland County, Connecticut, June 18, 1934, growing on living *Ulmus americana* L., in mixed deciduous woods. The tree had apparently suffered mechanical injury near the base, and the sporophores were growing from this region. This collection has been divided between the herbaria of the Connecticut State College and The New York Botanical Garden.

Negatively it should be noted that Maneval (**1926**) does not include *Polyporus squamosus* in his extensive list of parasitic and wood destroying fungi of Missouri. Also Anderson et al. (**1926**), while including *P. squamosus* as a parasite on *Acer Negundo* L., from Minnesota in their "Checklist of Diseases of Economic Plants in the United States," do not mention this species in connection with any other host nor from any other locality.

It is apparent that, while we have some knowledge regarding

the geographical distribution of this species in America, we have but little respecting its host range or host preferences. Actually *Polyporus squamosus* has now only been reported as parasitic on six host species within this region, and three of these are additions that have been made in this paper. It is unfortunate that, in the majority of the reports cited, the host has evidently been considered of negligible importance.

The synonymy of *Polyporus squamosus* and, as this would denote, its literature are not well known. For this reason I am including a reasonably complete synonymy. Aside from the species there are also three readily distinguishable varieties. One of these is solely European, one both European and American while the third seems to be confined to the United States.

1. POLYPORUS SQUAMOSUS (Huds.) Fries, Syst. Myc. **1**: 343. 1821.

Boletus squamosus Huds. Fl. Angl. Ed. 2, 626. 1778.

Auricula flammea Malchi Sterb. Theat. Fung. 105, *pl. 13*. 1675.

Agaricum squamosum, Ilicibus Mich. Nov. Plant. Gen. 118. 1729.

Boletus Juglandis Schaeff. Ic. Fung. Bavar. **2**: 101–102, *pl. 101–102*. 1763.

Polyporus sessilis Hall. Hist. Pl. Indig. Helv. 202. 1769.

Boletus caudicinus Scop. Flor. Carn. Ed. 2, **2**: 469. 1772.

Agaricus aureus Batt. Fung. Hist. 68, *pl. 37*, *fig. A–B*. 1775.

Boletus cellulosus Lightf. Flor. Scot. **2**: 1032. 1777.

Polyporus Ulmi Paulet, Traité Champ. **2**: 102. 1793.

Boletus platyporus Pers. Syn. Fung. 521. 1801.

Polyporus flabelliformis Pers. Myc. Eur. **2**: 53. 1825.

Polyporus tigrinus Pers. Myc. Eur. **2**: 54. 1825.

Polyporus squamosus (Huds.) Fries var. *crassipes* Kickx, Rech. Flor. Crypt. Fland. **5**: 46. 1855.

Polyporus squamosus (Huds.) Fries var. *laevipes* Kickx, Rech. Flor. Crypt. Fland. **5**: 47. 1855.

Polyporus squamosus (Huds.) Fries var. *aureus* Kickx, Flor. Fland. **2**: 223. 1867.

Bresadolia paradoxa Speg. Anal. Soc. Sci. Argent. **16**: 15. 1883.

Cerioporus squamosus (Huds.) Quél. Ench. Fung. 167. 1886.

Melanopus squamosus (Huds.) Pat. Hymen. Eur. 137. 1887.

Polyporus squamosus (Huds.) Fries, f. *erecta* Bres. Fung. Trid. **2**: 27, *pl. 133*. 1892.

Polyporus caudicinus (Scop.) Murr. Jour. Myc. **9**: 89. 1903.

Bresadolia caucasica Schest. in Magnus, Hedwigia **50**: 101, *pl. 2*. 1911.

Basidiocarps large, solitary or in imbricated, caespitose clusters; pileus dimidiate, reniform or becoming flabelliform, 5–40 cm. broad, 0.5–4 cm. thick; surface smooth, ochraceous-yellow to brown or fulvous, covered with large, appressed, dark brown scales which may be close together in young specimens but further apart in older plants; margin thin, involute, slightly wavy, entire; context thin, white when fresh, soft and fleshy when young, becoming tough-fleshy and drying spongy- to corky-fragile, homogeneous, 0.3–3.2 cm. thick, with hyaline, branching, thick-walled hyphae, 4–8 μ in diameter; tubes white to yellowish, darker on drying, at first shallow pits, developing into large, angular, favoloid pores, 8 mm. deep, 1–3 mm. tangential diameter, 1.5–6 mm. radial diameter, edges of dissepiments become thin, entire to dentate or lacerate at maturity, decurrent as shallow pits or reticulations; stipe lateral or excentric, rarely subcentral, 1–5 cm. long, 1–3 cm. thick, sometimes rudimentary, at first obese, white to yellowish or pale buff and reticulate-poroid above, black or dark brown and sometimes areolate below, solid, homogeneous, base somewhat bulbous; hymenium compact, 20–30 μ thick; basidia clavate, 8 μ broad; spores hyaline, smooth, elongate-ovoid to ellipsoid, apiculate, 12–16 $\times$ 4.5–6(14 $\times$ 5) μ; cystidia wanting; vegetative hyphae 6–8 μ in diameter.

TYPE LOCALITY: Northern England.

HABITAT: *Acer glabrum* Torr.; *Acer Negundo* L.; *Aesculus octandra* Marsh; *Populus trichocarpa* T. & G.; *Salix nigra* Marsh; *Ulmus americana* L.; also *Acer*, *Populus* and *Salix* species undetermined. Late spring and summer.

DISTRIBUTION: Rare in Massachusetts, Connecticut, New

York, Pennsylvania, West Virginia, North Carolina, Ohio, Michigan, Illinois, Missouri, Arkansas, Wisconsin, Minnesota, Iowa, Kansas, Montana, Colorado, the provinces of Ontario and Manitoba; very common in Europe; Altai, Mongolia, Asia (Burt); Queensland, Australia (Cooke); Paraguay, South America (Spegazzini).

ILLUSTRATIONS: Lloyd, Photo. Am. Fungi, *pl. 5.* 1897; McIlvaine, One Thousand Am. Fungi, *pl. 130.* 1900; Hard, Mushrooms, *fig. 325.* 1908; Duggar, Fung. Dis. Plants, *fig. 223–224.* 1909; Neuman, Wisc. Geol. Nat. Hist. Surv. Bull. **33**: *pl. 14, fig. 51b, pl. 15, fig. 51a.* 1914; Hesler, Jour. Tenn. Acad. Sci. 4: *fig. 2.* 1929; Shope, Ann. Missouri Bot. Gard. **18**: *pl. 29, fig. 1–2.* 1931.

Polyporus squamosus and its varieties cause a white heart-rot of timber. In Europe the loss due to this fungus is considerable because of the prevalence of the disease and its wide range of hosts. In the United States the loss is negligible because of the rarity of the fungus and greater host selectivity. With its spread, however, there is a potential danger. The fungus normally attacks living trees as a wound parasite, but habitually persists in a saprophytic state in fallen or felled timber and the remaining stumps.

While *Polyporus squamosus* has never been found a common species at any time, its presence in North America has been recognized since 1875, when it was first reported by Peck. In a number of the states enumerated but one collection has been reported and in several not more than two.

It will be noted that I have not given recognition to the upright growing form with a tendency toward an ochraceous-yellow color among the varieties of this species. Bresadola (**1892**) segregates this as forma *erecta* in his earlier work, but later (**1931**) concludes that this is unwarranted, though Kickx (**1867**) had previously given it varietal rank as var. *aureus*. This variation seems to be associated rather definitely with a saprophytic development. Collections to which the upright, infundibuliform growth and yellowish color have been ascribed appear to have been gathered from tree stumps or dead and more or less aged timber. It seems to me a purely ecological variation.

American specimens usually mature as single pileate plants, and are but rarely found developing in the caespitose manner that is apparently more usual in Europe. Nor do they reach the size reported from western Europe where the largest forms seem to have been collected. Specimens gathered in the United States rarely exceed 20–30 cm. in breadth. Clements (**1910**), in reporting *Polyporus squamosus* from Minnesota, says that it occurs occasionally on the ground in woods, and is said to attain a width of 7 feet and a weight of 40 pounds. Clements' record is of particular interest being the only time this fungus has been reported growing upon the ground. McIlvaine (**1900**), without any reference to locality, says that this species has been known to attain a circumference of 7 feet 5 inches, and a weight of 40 pounds.

In localities where this fungus is most prolific and variable many specimens of considerable size have been found. In eastern Europe a width of 50 cm. has been reported, and considered exceptionally large. To the westward, on the other hand, we find that large specimens are not infrequent, and that in England, Hooker (**1821**) reports a plant of this species which he says, "Has regularly made its appearance for several years past, on the stump of an ash, at Dalbeth, near Glasgow. In 1810 it attained an extraordinary size, being 7 feet 5 inches in circumference, and weighing, after having been cut four days, thirty-four pounds avoird."

In Fries' (**1828**) description of *Polyporus squamosus* the pores are described as at first minute, then large and angular. Lloyd (**1911**) offers objection to this, and gives as his opinion that they are "at first large, angular, shallow, merely large reticulations in fact, and really become smaller in diameter as they grow in depth."

From my own observations, based upon freshly gathered material, it appears that the pores are at first shallow and separated from one another by relatively broad dissepiments, thus causing them to appear small. Approaching maturity, these dissepiments grow in length and become very thin. As a result of this the pores present the appearance of increasing in diameter as well as depth. It is true that these irregular pores

may become apparently larger by the partial breaking down, or cessation in growth, of a wall before reaching its mature length. In this manner a merging of adjacent pores may take place. This, however, only occurs at rare and very scattered intervasl. As for becoming smaller in diameter as they grow in depth, this could only apply to old specimens that are drying with an accompanying shrinkage and curling of the pileus. Lloyd says that his observations were based upon dried specimens.

The upper surface of *Polyporus squamosus* reminds one most strikingly of *Lentinus lepidus* Fries. Fries recognized this and says in his discussion, "*Ag. lepidei*, cui haec species analoga, similis." In pore character there is a distinct trend toward the genus *Favolus*.

2. POLYPORUS SQUAMOSUS (Huds.) Fries, var. **polymorphus** (Bull.) comb. nov.

Agaricus ramosus cornu reniferi referens Blacks. Specim. Bot. Plant. Angliae 2, *pl. 1*. 1746.

? Clavaria Hypoxylon var. *B*. Huds. Flor. Angl. Ed. 2, **2**: 639. 1778.

Boletus polymorphus Bull. Herb. France *pl. 144, fig. A*. 1782.

Boletus rangiferinus Bolt. Hist. Fung. Halifax **3**: 138, *pl. 138*. 1789.

Having much elongated and somewhat curved stipes, which may branch irregularly several times, while the pilei are proportionately reduced in size. The basidiocarp, as a whole, is very irregular and sometimes quite dendroid in form. The pilei, in extreme cases, may be of the same, or only slightly greater, diameter as the stipe, or may even be in part wanting. There is, however, much variability in this respect. The pores are often less favoloid than in the species, being more shallow and having thicker dissepiments. Otherwise the characters are the same as those of the species.

TYPE LOCALITY: France.
HABITAT: Dead and fallen timber, and stumps.
DISTRIBUTION: England, France.

ILLUSTRATIONS: Blackstone, Specim. Bot. Plant. Angliae, *pl. 1.* 1746; Bolton, Hist. Fung. Halifax **3**: *pl. 138.* 1789; Bulliard, Herb. France *pl. 144, fig. A.* 1782; Sowerby, Engl. Fungi **3**: *pl. 266.* 1803.

Blackstone (**1746**) has apparently given us one of the earliest descriptions of this variety. He has also given us, in his first plate, a very characteristic illustration of this interesting fungus. Of his specimen, he says, "This elegant Species was found in 1744, growing on an old Elm Stump, in a Smith's Cellar in the Haymarket, London," and further speaks of it as a branched Agaric, resembling the horn of a Reindeer.

Bulliard's (**1782**) fungus is not of the extreme type described by Blackstone and later by Bolton, and yet, in the form of stipe and pileus, is far from having the appearance of the typical plant. On the same plate with his *Boletus polymorphus* he shows, for comparison, the regular form under the name *Boletus Juglandis.*

Bolton (**1789**) describes at considerable length a similar fungus under the common name of "Rain-Deer Boletus." He says that this species, which he proposes to name *Boletus rangiferinus,* is the same as the fungus figured by Blackstone, and also the same as Hudson's *Clavaria Hypoxylon* var. *B.* There can be no doubt that it is the same as Blackstone described. Whether Hudson's *Clavaria* is also the same thing will probably remain questionable.

The specimen upon which Bolton's description is based was found growing upon an old log in the town of Leeds. His plate shows a plant with a much elongated, branching stipe, in some cases terminated by small, apparently abortive, pilei, while on others even these are lacking. Two of the latter display finger-like branches toward the ends. A few branches have fairly well formed pilei. All branches have their origin in a common base.

As Sowerby (**1803**) has pointed out, *Polyporus squamosus* is one of the most mutable species among European polypores. It is for this reason, he asserts, that Bulliard was justified in giving this form of the fungus the name he proposed. In his *plate 266* Sowerby gives figures of both typical and rangiferoid forms of the species.

Hussey (**1847**), while discussing *Polyporus squamosus,* says

that monstrous specimens of *Polyporus*, prevented from natural expansion into true pilei, have been erroneously considered as distinct species, and variously named accordingly, and that *Boletus rangiferinus* is one of these.

Sowerby expresses the view that these branching forms with reduced pilei are but terratological representatives of the species. Personally I would be inclined to accept these opinions of Hussey and Sowerby were it not for the fact that this variety is apparently limited in its distribution to western Europe. No collection has thus far been reported outside of this restricted area. This limitation in a variety, when the species is widely distributed, would seem significant. While this variety may be merged with the species in time, I do not believe our present data are sufficient to permit such action.

3. POLYPORUS SQUAMOSUS (Huds.) Fries, var. **glaber** (Batt.) comb. nov.

Agaricus squamosus glaber Batt. Fung. Hist. 68, *pl. 34, fig. A*. 1775.

Poria vaporarius Pers. Obs. Myc. **2**: 15. 1799.

Boletus vaporarius Pers. Syn. Fung. 546. 1801.

Polyporus vaporarius (Pers.) Fries, Syst. Myc. **1**: 382. 1821.

Polyporus infundibuliformis Rost. in Sturm. Deuts. Flora **3**: 37, *pl. 17*. 1831.

Polyporus Rostkowii Fries, Epicr. 439. 1838.

Polyporus pallidus Schulz. & Kalchbr. in Kalchbr. Ic. Hymen. Hung. *pl. 38, fig. 2*. 1877. Not Berk. 1856.

Polyporus pennsylvanicus Sumst. Jour. Myc. **13**: 137. 1907.

Pileus solitary to caespitose with several stipes connate at the base, subcircular to reniform, sometimes infundibuliform, 3–15 cm. broad, 0.5–2 cm. thick; surface smooth, without scales or fibrils, light tan, occasionally smoke-colored; margin thin, wavy, entire; context white to pallid, soft-fleshy to punky, fragile when dry, 0.2–1 cm. thick, of usually sparsely branched, thick walled hyphae, 3–9 μ in diameter; tubes white to yellowish, large, angular, favoloid, 2–6 mm. long, 1–2.5 mm. wide, edges of dissepiments thin, entire, lacerate or toothed, decurrent; stipe excentric to lateral, 2–5 cm. long, 1–2.5 cm. thick, pallid to

reddish with black stains, occasionally abruptly black, upper portion reticulated by the rudimentary, decurrent tubes; spores hyaline, elongate-ellipsoidal, 11–16 × 4–6 (14 × 5), smooth; cystidia wanting.

TYPE LOCALITY: Rimini, Italy.

HABITAT: Wood of deciduous trees. Late spring and summer.

DISTRIBUTION: Rare in New York, Pennsylvania, Ohio: Rare in Europe.

ILLUSTRATIONS: Battarra, Fung. Hist. *pl. 34, fig. A.* 1775; Kalchbrenner, Ic. Hymen. Hung. *pl. 38.* 1875; Sturm, Deuts. Fl. Pilze **3**: *pl. 17.* 1831.

Battarra (**1775**) first described this fungus as a glabrous variety of *Agaricum squamosum* Mich. It therefore becomes necessary, for reasons previously mentioned, to combine Battarra's varietal name with *Boletus squamosus* Huds.

American material is usually found solitary and ranges from 4–10 cm. in width, with a stipe 2–4 cm. long by 1–1.5 cm. thick that is more often pallid throughout but may become reddish with black stains. On the other hand European specimens, and especially those from England, are more often caespitose, approach the species in size and may have its definite black based stipe.

Peck (**1879**) has referred his New York material to *Polyporus pallidus* Schulz. & Kalchbr., while Lloyd (**1911**), who has examined the same specimens, says that they agree with his conception of *P. Rostkowii* Fries. This does not conform with the opinion of Bresadola (**1931**), who considers that *P. pallidus* is the same as the *aureus* form of the species. It would be difficult to agree with Bresadola after consulting Kalchbrenner's (**1877**) publication.

Fries (**1838**) recognized a definite relationship between his *Polyporus Rostkowii* and *P. squamosus*, and says in this connection, "Magnitudine cum affini *P. squamoso* certat."

4. POLYPORUS SQUAMOSUS (Huds.) Fries, var. **fagicola** (Murr.) comb. nov.

Polyporus fagicola Murr. Torreya **6**: 35. 1906.

Pileus circular to subcircular, convex to plane and umbilicate, 4–8 cm. broad, 0.1–0.5 cm. thick; surface smooth, light yellow-

brown to pale brown, with tufts of innate fibrils which are larger and darker near the center and more scattered toward the periphery, though sometimes almost wanting; margin very thin, slightly decurved, regular, not ciliate; context white, fibrous, 1–4 mm. thick, composed of hyphae 3–10 μ in diameter, usually thin walled but variable in this respect, when thin walled more frequently branching than when thick walled; tubes white or whitish, favoloid, 1–2.5 mm. long, 0.5–1.5 mm. wide, decurrent; stipe central to excentric, solid, thick, conspicuously hispid, particularly toward the base, 2–4 cm. long, 1–1.5 cm. thick, white or whitish, rarely brownish or darkened at the base, upper portion reticulate with decurrent tubes; spores hyaline, elongate-ellipsoidal, 11–15 $\times$ 4–5(14 $\times$ 4.5) μ, smooth.

TYPE LOCALITY: Boarstone Mountain, Piscataquis County, Maine.

HABITAT: *Fagus grandifolia* Ehrh.

DISTRIBUTION: Maine, New York.

ILLUSTRATIONS: Lowe, Mich. Acad. Sci. **19**: *pl. 15, fig. 3–4.* 1933.

Murrill (**1906, 1908**) reports the spore size as 6–7 $\times$ 3–4 μ in his original description and subsequent publication. This is much smaller than that of the spores of *Polyporus squamosus* and its varieties. I find, upon examination of Murrill's type material, however, the spore measurement to be 11–15 $\times$ 4–5.5 (14 $\times$ 5) μ, in the case of mature spores, and hence comparable to those of the above named species. My findings agree in this respect with those already reported by Lowe (**1934**) who has also examined Murrill's type specimen. There is but one specimen of this fungus in the herbarium of The New York Botanical Garden. This is very evidently young material, and it seems possible that Murrill's error may have been due to an examination of spores from near the immature margin. Had the spores been found to vary as much as Murrill suggests there might be sufficient reason for considering this a distinct species. Without this the segregation seems unwarranted, and varietal standing more desirable.

Lowe (**1933**) believes the chief difference between *Polyporus fagicola* and *P. pennsylvanicus* to be in the absence of scales on the pileus and the larger pores of the latter species. He believes that *P. pennsylvanicus* should be placed in synonymy with

P. fagicola which he considers merely a diminutive form of *P. squamosus*. Lowe does not recognize the possibility of a closer relationship between *P. pennsylvanicus* and the forms included in the earlier synonymy as I have presented it in the present paper.

It seems to me that the purposes of taxonomy are better served by including *Polyporus pennsylvanicus* and the American forms previously recognized as *P. pallidus* or *P. Rostkowii* with the European glabrous forms. It may be granted that these are usually smaller in size than the members of this variety found in Europe, but the same may be said for American material of the species itself.

Polyporus fagicola varies from *P. squamosus* in its typically much smaller pileus, in the fact that its cap scales are reduced to hairs and in its smaller pores. It is in all respects, except with regard to spores, a diminutive variety of *P. squamosus*. It seems to me that *P. fagicola* has developed along a somewhat different line of divergence from the species than those forms which I have recognized as var. *glaber*, and should for that reason be kept distinct.

There is apparently another American form of *Polyporus squamosus* which is in need of investigation. Though I have seen but one collection of this variety, it appears to have such marked characteristics as to arouse one's curiosity. The specimens which I have observed have the diagnostic characteristics of the species except that the color of the upper surface is distinctly grayish as well as being radially striate. This material has the size, the surface scales, large favoloid pores and the dark based stipe of *P. squamosus*, but with a surface color suggestive of a quite different species provided the scales were removed.

Polyporus arcularius Batsch, with its brown, minutely scaly cap, favoloid tubes and dark brown stipe would seem to be remotely related to the smaller forms of *P. squamosus*. Its smaller spores and other varying characteristics prevent its inclusion here and indicate that it should be retained as a separate species.

The writer wishes to express his indebtedness to Dr. F. J. Seaver and The New York Botanical Garden for courtesies extended during the preparation of this paper.

LITERATURE CITED

Anderson, P. J. et al. 1926. Check-list of diseases of economic plants in the United States. U. S. Dept. Agric. Bull. 1366: 1–111.

Battarra, G. A. 1775. Fungorum agri ariminensis historia 1–80, *pl. 1–40*.

Bisby, G. R., Buller, A. H. R., Dearness, J. 1929. The fungi of Manitoba 1–194.

Blackstone, J. 1746. Specimen botanicum quo plantarum plurium rariorum Angliae 1–106, *pl. 1–2*.

Bolton, J. 1789. An history of fungusses, growing about Halifax **2**: 45–92, *pl. 45–92*.

——. 1791. Ibid. **3**: 93–138, *pl. 93–138*.

Bresadola, J. 1892. Fungi Tridentini **2**: 1–46, *pl. 106–150*.

——. 1931. Iconographia mycologica **20**: *pl. 951–1000*.

Bulliard, P. 1782. Herb. France *pl. 97–144*.

——. 1790. Ibid. *pl. 481–528*.

Clements, F. E. 1910. Minnesota plant studies, IV. Minnesota mushrooms 1–169, *pl. 1–2, fig. 1–124*.

Clusius, C. 1601. Fungorum in Pannoniis observatorum historia. Rariorum plantarum historia cclxi–ccxcv.

Craigin, F. W. 1884. First contribution to the catalogue of the Hymenomycetes and Gastromycetes of Kansas. Bull. Washb. Lab. Nat. Hist. **1**: 19–28.

Dillenius, J. J. 1718. Catalogus plantarum circa Gissam sponte nascentium 1–240, *pl. 1–12*.

Dodge, B. O. 1914. A list of the fungi of Kewaunee County, Wisconsin. Trans. Wis. Acad. Sci. **17**: 806–845.

Fries, E. M. 1828. Elenchus fungorum **1**: 1–238.

——. 1838. Epicrisis systematis mycologici 1–610.

Haller, A. v. 1768. Historia plantarum indigenarum Helvetiae 1–216.

Harzer, C. A. F. 1845. Naturgetreue Abbildungen der vorzüglichsten essbaren, giftigen und verdachtigen Pilze 1–136, *pl. 1–80*.

Hooker, W. J. 1821. Flora Scotica **2**: 1–296.

Hudson, W. 1778. Flora Anglica Ed. 2, 1–690.

Hussey, T. J. 1847. Illustrations of British mycology **1**: 1–90, *pl. 1–90*.

Kalchbrenner, K. 1877. Icones selectae Hymenomycetum Hungariae 1–66, *pl. 1–40*.

Kauffman, C. H. 1917. Unreported Michigan fungi for 1915 and 1916. Mich. Acad. Sci. Rep. **19**: 145–157.

Kickx, J. 1867. Flore cryptogamique des Flandres **2**: 1–490.

Lloyd, C. G. 1911. Synopsis of the section Ovinus of *Polyporus* 73–93, *fig. 496–509*.

Lowe, J. L. 1933. Notes on some species of *Polyporus*. Papers Mich. Acad. Sci. **19**: 141–148, *pl. 14–15*.

——. 1934. The Polyporaceae of New York State. N. Y. State Coll. For. Bull. 41: 1–142, *pl. 1–2*.

McIlvaine, C. 1900. One thousand American fungi 1–740, *pl. 1–182*.

Maneval, W. E. 1926. Parasitic and wood-destroying fungi of Boone County, Missouri. Univ. Missouri Stud. **1**: 63–111.

Micheli, P. A. 1729. Nova plantarum genera 1–234, *pl. 1–108*.

Murrill, W. A. 1903. A historical review of the genera of the Polyporaceae. Jour. Myc. **9**: 87–102.

——. 1904. The Polyporaceae of North America. VI. The genus *Polyporus*. Bull. Torrey Club **31**: 29–44.

——. 1906. The pileate Polyporaceae of Central Maine. Torreya **6**: 34–37.

——. 1908. Polyporaceae. N. Am. Flora **9**: 1–131.

Neuman, J. J. 1914. The Polyporaceae of Wisconsin. Wis. Geol. Nat. Hist. Surv. Bull. 33: 1–156, *pl. 1–25*.

Overholts, L. O. 1914. The Polyporaceae of Ohio. Ann. Missouri Bot. Gard. **1**: 81–155.

——. 1915. The Polyporaceae of the middle-western United States. Wash. Univ. Studies **3**: 1–83, *pl. 1–8*.

——. 1933. The Polyporaceae of Pennsylvania. Penn. Agr. Exp. Sta. Bull. 298: 1–28, *pl. 1–2*.

Peck, C. H. 1875. Report of the Botanist for 1873. .Ann. Rep. N. Y. State Mus. **27**: 73–113, *pl. 1–2*.

——. 1879. Report of the Botanist for 1877. Ann. Rep. N. Y. State Mus. **31**: 19–60.

Schaeffer, J. C. 1763. Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icones **2**: 101–200, *pl. 101–200*.

Scopoli, J. A. 1772. Flora carniolica Ed. 2, **1**: 1–496, *pl. 33–65*.

Shope, P. F. 1931. The Polyporaceae of Colorado. Ann. Missouri Bot. Gard. **18**: 287–456, *pl. 16–39*.

Sowerby, J. 1803. Colored figures of English fungi or mushrooms **3**: *pl. 241–400*.

Sterbeck, F. v. 1675. Theatrum fungorum, oft Het Poonel der Campernoelien 1–396, *pl. 1–36*.

White, E. A. 1905. A preliminary report on the Hymeniales of Connecticut. Conn. Geol. Nat. Hist. Surv. Bull. 3: 1–81, *pl. 1–40*.

A LEAF-SPOT DISEASE OF HONEY LOCUST CAUSED BY A NEW SPECIES OF LINOSPORA

JULIAN H. MILLER AND FREDERICK A. WOLF

(WITH 2 FIGURES)

A fungus commonly designated as *Melasmia hypophylla* (B. & Rav.) Sacc. occurs on honey locust, *Gleditsia triacanthos* L., within the environs of Durham, North Carolina, and Athens, Georgia. From the records of collections it appears to be widely distributed throughout the southern United States. It is apparently restricted to this one host and does not appear on related leguminous plants.

The previous systematic position of this fungus has been within the family *Leptostromataceae* of the *Fungi Imperfecti*. It was first described as *Sacidium Gleditschiae*, in 1845, by Léveillé (**7**: 64) from specimens collected in Texas and deposited in the Museum of Paris. Subsequently, it was collected in South Carolina by Ravenel who sent specimens to Berkeley in 1855, and they designated it *Leptostroma hypophyllum* B. & Rav., but apparently they never described it. Ravenel distributed it under this name in Fungi Caroliniana fasc. III, no. *45*. In 1888, specimens of this same fungus were communicated to Ellis and Everhart (**3**: 45) from Missouri, Kansas, and Louisiana, and it was again renamed, this time being assigned the binomial, *Melasmia Gleditschiae*. Saccardo (**9**: 419), in 1892, recognized that *Leptostroma hypophyllum* and *Melasmia Gleditschiae* are synonymous, but he was not aware that *Sacidium Gleditschiae* applies to the same organism, and in consequence employed *Melasmia hypophylla* (B. & Rav.) Sacc. as the name of this pathogene on honey locust. Seymour (**10**) employed *Melasmia Gleditschiae* (Lév.) Ellis & Ever. as the most acceptable name. Apparently, these brief mycological notes constitute all that has been published regarding this fungus during the period since 1845 when it was first described.

The writers' studies have been concerned with the structure of the pathogene, both conidial and perithecial stages, as a basis for determining its systematic position. The type of development of the organism, as determined by examination of infected leaves at intervals throughout the summer and fall, shows that it is questionable whether the conidial stage should be regarded as *Melasmia*. The perithecial stage, that matures in spring on decaying leaves, has not been described previously. The honey locust organism has been compared with European specimens of *Linospora Capreae* (DC. ex F.) Fuckel, the type of the genus *Linospora* on *Salix caprea*, and has been found to conform closely to it.

CONIDIAL STAGE

The fungus, in its conidial stage, can be recognized by the presence of numerous, flat, black fructifications upon the lower leaf surface. They may occupy the greater part of the lower leaf surface, or be densely scattered over it (FIG. 1, 2*A*). They vary in size from mere points to bodies 1 mm. in diameter. When discrete they are circular, and are irregular when several have coalesced. If the fructifications are examined with a binocular, irregular fissures, through which the conidia are liberated, are apparent. Tissues that are embedded in paraffin and viewed in vertical section (FIG. 2*B*) clearly show that the fruiting structures are subcuticular, and that the conidia arise from a thin palisade layer that is seated upon the epidermal cells. The cuticle of the leaf above the conidial stroma becomes distended as the mass of spores increases, and the pressure thus produced eventually causes the cuticle to rupture. The conidia are oblong, straight, or slightly curved, hyaline and non-septate, measuring 3–5 × 1–1.5 μ (FIG. 2*F*). They are budded off singly from short conidiophores that form a compact palisade layer arising from the stroma.

This type of fructification is definitely not a pycnidium, but an acervulus. *Melasmia*, according to the generic concept, consists of a pycnidium within a stroma that opens with a longitudinal slit, and the spore layer is definitely inclosed by fungous tissue. In contrast with this, the acervulus of the honey locust fungus is composed of a parallel layer of conidiophores developing from a subhymenial stromatic layer. The layer comprising the cover of the

fruit body contains no fungous tissue but consists solely of the leaf cuticle. These morphological features place this imperfect stage within the order *Melanconiales*, family *Melanconiaceae—Hyalosporae*, and in the form genus *Gloeosporium*.

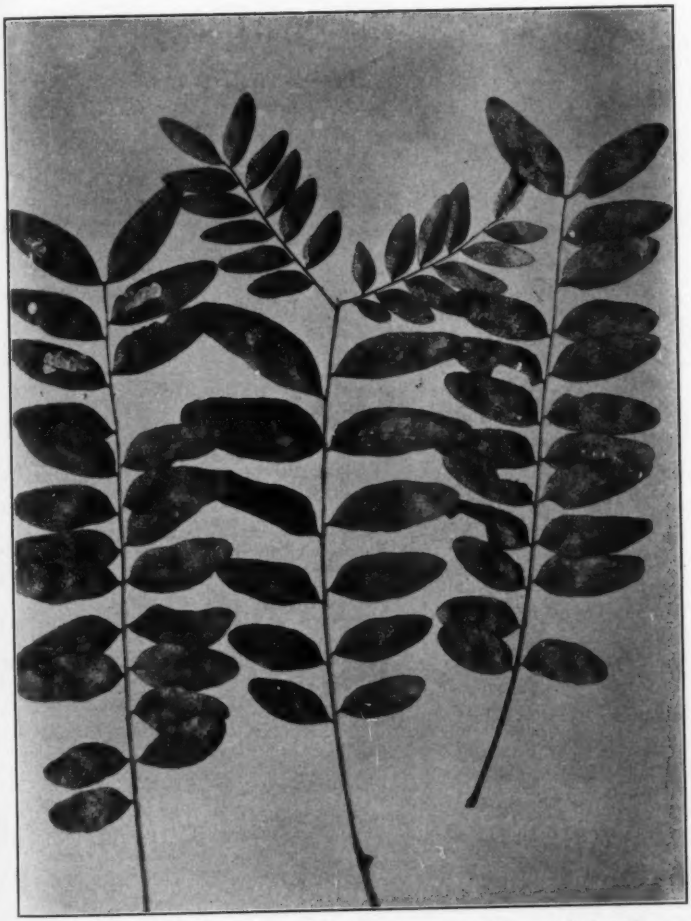

FIG. 1. Leaves of honey locust showing acervuli of the so-called *Melasmia* stage of *Linospora Gleditsiae*.

THE PERITHECIAL STAGE

The perithecial stage was collected in 1933, and again in 1934, and appears to be mature throughout the period from the middle of May until the middle of August. It can be recognized by the blunt, cylindrical, perithecial beaks that project prominently, usually from the upper leaf surface of infected leaves found in moist places under the trees. There are from a few to approximately twenty, occurring singly or in pairs, on each leaflet. Leaves cut in vertical section show that the perithecia are embedded within the mesophyll, and that they are so large that the leaf is distended. The axes of the perithecia are parallel to the leaf surface, and the beaks are so bent as to be perpendicular to the leaf surface (FIG. 2*C*).

The perithecial initials were first seen within the mesophyll of leaf sections of material collected in December. At this time they consist of spherical masses of very fine hyphae inclosing larger elements in a rather loose center. During the winter the peripheral layer of hyphae expands rapidly. The divisions are chiefly tangential, resulting in the increase in diameter of the mass, without any apparent increase in the thickness of the wall.

The ostiolar neck begins as a vertical cone in the apex of the perithecium, and is directed toward the leaf center, rather than toward the leaf surface. Then, during the latter part of February and March, the wall cells proliferate inward forming a beak that bends upward during development and that finally pierces the epidermis. The perithecial wall now consists of very fine coalesced hyphae that course peripherally and into the tissue of the lateral beak. At maturity this beak measures from 0.5 to 1.5 mm. in length, and appears on the side of the leaf opposite that in contact with the soil.

At an early stage the perithecial centrum consists of true paraphyses with free ends pointing toward the upper center of the cavity. There is a continuation of these elements in the beak as the wall apex grows upward. Here, however, the threads are very much finer, and when the beak is mature they form the true periphyses of the ostiolar cavity. These periphyses, and the paraphyses on the upper wall adjacent to the opening, are perma-

nent, but those paraphyses interspersed with the asci are digested and disappear as the asci mature.

The ascogenous hyphae lie on the inner periphery at the base and sides of the perithecial wall. Their penultimate cells become the asci, which grow upward among the paraphyses. When mature, the asci are cylindrical, straight or curved, with no stipe, and inclose eight filiform ascospores (FIG. 2*D*). The bases of the asci are readily soluble in water, and in free hand sections the entire mass of asci separates, as in species of *Diaporthe*. The mature perithecial centrum consists of asci lining the base and sides, directed toward the lateral aperture of the ostiolar neck.

There is no fungous structure within the leaf that one could term a stroma or that appears like the coalesced hyphae which one finds in the *Xylariaceae*. The entire mesophyll of the leaf, however, contains a much branched hyphal system, both inter- and intra-cellular. These threads are dark, have extremely thick walls, and a very small lumen. Within the epidermal cells, they form a pseudoclypeus which is penetrated by the beak.

If the leaves are kept moist the asci are extruded in droplets at the tips of the beaks. This type of ascal discharge has been observed in several genera of long beaked Pyrenomycetes, and has been described by Ingold (**5**: 177), in the case of *Ceratostomella ampullasca* (Cooke.) Sacc. The asci are usually curved, and are provided with a thickened apical wall that is partly pierced by a tubular pore (FIG. 2*D*). The asci measure 80–110 × 10–15 μ. The ascospores are filiform, hyaline, and 70–90 × 3 μ (FIG. 2*E*).

Attempts to cultivate this organism on artificial media have thus far not been successful. Both conidia and ascospores have failed to germinate. When, however, in July 1934, leaflets bearing the perithecial stage were fastened to healthy leaflets, infection followed, and the conidial stage had developed within four or five weeks after inoculation. This demonstrates the genetic connection of the ascigerous and conidial stages.

The increase in the number of diseased leaflets, on trees that were observed at frequent intervals, indicates that the conidia must be capable of germination. It may be recalled that Jones (**6**: 41) suggested that the so-called conidia of *Rhytisma acerinum* may be spermatia instead of conidia.

SYSTEMATIC POSITION OF THE FUNGUS

The presence of a special perithecial wall composed of fine hyphae that proliferate into a true ostiolar neck, and the presence of paraphyses and periphyses place the honey locust organism among the *Sphaeriales*. Those forms that appear similar to the fungus under consideration have no paraphyses and fall into one or the other of two developmental types. In one type, illustrated by *Dothidea collecta* (Schw.) Ell. and by species of *Mycosphaerella*, the asci grow upward and displace the parenchymatous tissue that comprises the center of the developing perithecium. In the other, illustrated by *Plowrightia morbosa* (Schw.) Sacc., and by members of the *Pleosporaceae*, the asci arise at the bases of parallel hyphae that are attached both at the top and bottom of the perithecial locule.

According to Clements and Shear (**2**: 59) the order *Sphaeriales* has family rank, *Sphaeriaceae*. In their *Scolecosporae* (**2**: 74) those fungi with a clypeus, without paraphyses, and with a lateral beak, are included in *Linospora;* those without a beak are placed in *Ceuthocarpon*. The type of *Linospora* is *L. Capreae* (DC. ex F.) Fuckel, and of *Ceuthocarpon* is *C. populinum* Pers. ex Karst. The writers have examined European specimens of both species: Exsic. 735 Petrak Fl. Bohem. et Morav., *Linospora Capreae* (DC.) Fuckel on *Salix caprea;* and Exsic. *246* Syd. Myc. Germ. *Linospora populina* (P.) Schröt. on leaves of *Populus tremula*. Both contain perithecia with prolonged lateral beaks, a blackened layer in the epidermis surrounding the beaks, and periphyses in the ostiolum, but paraphyses that disappear at maturity. These two forms, therefore, are clearly congeneric, as is concluded by Lindau in Engler und Prantl (**8**: 452). According to the generic concept used in the classification of Lindau the fungus on honey locust should be placed in the genus *Linospora* Fuckel, but in the family *Clypeosphaeriaceae*.

Another possible relationship of our fungus is with the genus *Ophiodothella* v. Höhn. Boyd (**1**: 463) transferred this genus from the *Phyllachoraceae* of the *Dothideales* to the *Clypeosphaeriaceae*. This genus is similar to *Linospora* in having a clypeus, perithecial wall, ostiolum, and periphyses and paraphyses, but differs in having papillate ostiola rather than a beaked ostiolum, and in the

manner of development of the ostiola. In *Linospora*, the ostiole is lateral and then bends upward, while in *Ophiodothella* it begins in the center of the top of the developing perithecium and grows straight upward. This difference in the ostiolar neck is regarded as sufficient to maintain the two genera as distinct.

When the present aggregation of unrelated forms is rearranged according to phylogenetic relationships *Linospora* should be grouped with the *Diaporthaceae* v. Höhn. Here the asci have no definite stalks and when moistened contract and dissolve, thus freeing the asci from each other. The ascus walls readily dissolve in the *Diaporthaceae*. The paraphyses are delicate, numerous, and evenescent with age, but the periphyses remain. These characteristics represent the concept of von Höhnel (**4**: 631), and also that of Wehmeyer (**11**: 610). The *Clypeosphaeriaceae* and *Diaporthaceae*, as now understood, are separated mainly on the grounds that one occurs on bark, the other on leaves; and that the stroma is better developed in one than in the other. These do not appear to be adequate reasons for separation into two families.

The conidial stages in species of *Linospora* are not well known. The writers find no mention of conidial stages for *L. Capreae*, but *L. populina* has a *Gloeosporium* stage very much like that in *L. Gleditsiae*.

DESCRIPTION OF THE FUNGUS

The developmental morphology of the perithecial stage, as well as that of the conidial stage, definitely places this fungus in the genus *Linospora* Fuckel of the family *Clypeosphaeriaceae*. It is proposed that the organism under consideration be given a new name. It is briefly characterized as follows:

Linospora Gleditsiae n. sp.[1]

Syn. *Sacidium Gleditschiae* Lév. Ann. Sci. Nat. III. **3**: 64. 1845.

Leptostroma hypophyllum B. & Rav.

Exsic. Rav. Fung. Car. **3**: *45*. 1855.
Ellis & Ever. N. A. F. *2173*. 1889.
Seymour & Earle, Econ. Fung. *123*. 1892.
Ellis & Ever. Fung. Columb. *975*. 1896.

[1] From data kindly supplied by Dr. Grant D. Darker, Farlow Herbarium, Cambridge, Massachusetts.

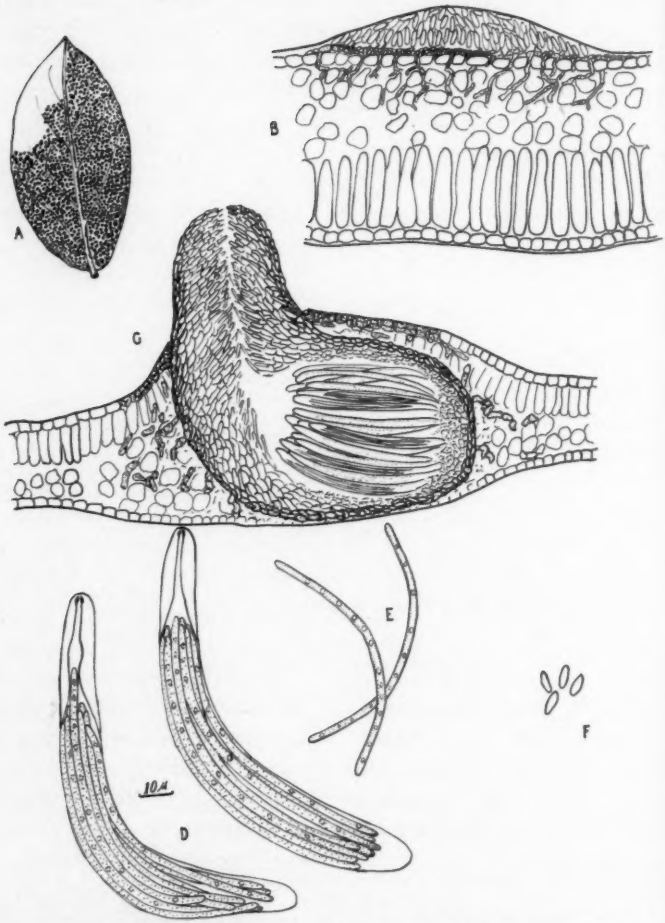

FIG. 2. A, diagram of leaflets showing the distribution of acervuli on the lower leaf surface; B, acervulus, in vertical section, formed between the epidermal cells and the cuticle; C, vertical section of the perithecium of *Linospora Gleditsiae* embedded within the mesophyll and with bent beak and asci parallel to the leaf surface; D, asci of *L. Gleditsiae;* they lack stipes and possess apical pores (D, E, and F drawn to scale shown near the asci); E, ascospores; F, conidia.

Melasmia Gleditschiae Ellis & Ever. Jour. Myc. **4**: 45. 1888.

Melasmia hypophylla (B. & Rav.) Sacc. Syll. Fung. **10**: 419. 1892.

Exsic. Pazschke Fung. Eur. *4196*. 1898.
Kellerm. Ohio Fung. *102*. 1903.
Kabat & Bubak Fung. Imp. *179*. 1904.
Barthol. Ell. & Ev. Fung. Columb. *975*. *2233* in index 26. 1910.

Melasmia Gleditschiae (Lév.) Ellis & Ever.

Exsic. Kellerm. & Sw. Kan. Fung. *10*. 1889.
Roum. Fung. Gall. *5039*. 1889.
Wilson & Seaver. Ascom. *13*. 1907.

Peritheciis sparsis, vulgo solitariis, folia pustulatim inflantibus, atris, procumbentibus, elongatis, rostris exsertis, atque curvulis; mycelio fusco in stratis epidermidis pseudoclypeum formante; rostris conicis, perithecio aequantibus vel longioribus; peritheciis in medio mesophyllio immersis; centrum peritheciale primitus ex paraphysibus atque ascibus constitutum, periphysibus in ostiolo, deinde paraphysibus disparentibus; ascis numerosis, sessilibus, oblongo-cylindraceis curvulis, 8-sporis, poro distincto praeditis, apice ostioli liberatis vel in aqua separabilibus, 80–110 × 10–15 μ; ascosporis filiformibus, hyalinis deinde virentibus, curvatis, poro liberatis vel parietibus basilaribus in aqua solutis, 70–90 × 3 μ.

Hab. in foliis dejectis atque putrescentibus *Gleditsiae triacanthi*, in terra.

Status conidicus: Acervulis hypophyllis, maculam fuscobrunneam occupantibus, dense punctiformibus, minutis vel 1 mm. diam.; orbicularibus vel irregularibus, subcuticularibus, atris; conidiis oblongis, rectis v. curvulis, continuis, hyalinis, 3–5 × 1–1.5 μ. Parasitice in foliis vivis, in aestive et autumne, *Gleditsiae triacanthi*.

Type specimens have been deposited in the Farlow Herbarium, Harvard University, Cambridge, Massachusetts.

SUMMARY

The conidial stage of a fungus of common occurrence on the foliage of honey locust has been known as *Melasmia hypophylla*. Its fructification is an acervulus and not a pycnidium, and it belongs in the form genus *Gloeosporium*.

The perithecial stage, described as *Linospora Gleditsiae* develops on diseased leaves that have overwintered. Evidence of genetic connection of the two stages is based upon the development of the conidial stage on leaves that were inoculated, using

leaves bearing perithecia as inoculum. Attempts to grow *Linospora Gleditsiae* in culture, either from ascospores or from conidia, have been unsuccessful.

It would seem that the genus *Linospora*, although in the *Clypeosphaeriaceae*, should better be placed nearer members of the *Diaporthaceae*.

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LITERATURE CITED

1. **Boyd, E. Sophia.** A developmental study of a new species of *Ophiodothella*. Mycologia **26**: 456–468. 1934.
2. **Clements, F. E. & Shear, C. L.** The genera of fungi. H. W. Wilson Co., New York. 1931.
3. **Ellis, J. B. & Everhart, B. M.** New species of fungi from various localities. Jour. Myc. **4**: 44–46. 1888.
4. **Höhnel, F. von.** System der Diaportheen. Ber. Deutsch. Bot. Ges. **35**: 631–638. 1927.
5. **Ingold, C. T.** Spore discharge in the Ascomycetes. New Phytol. **32**: 177–196. 1933.
6. **Jones, S. G.** Life history and cytology of *Rhytisma acerinum* (P.) Fr. Ann. Bot. **39**: 41–75. 1925.
7. **Léveillé, J. H.** Champignons exôtiques. Ann. Sci. Nat. III. **3**: 38–71. 1845.
8. **Lindau, G. in Engler, A. & Prantl, K.** Nat. Pfl. 1, **1**: 1897.
9. **Saccardo, P. A.** Sylloge fungorum **10**: 419. 1892.
10. **Seymour, A. B.** Host index of the fungi of North America. 732 pp. 1929.
11. **Wehmeyer, L. E.** Biologic and phylogenetic study of the stromatic Sphaeriales. Am. Jour. Bot. **13**: 575–645. 1926.

A NEW PSEUDODISCOSIA [1]

RODERICK SPRAGUE AND A. G. JOHNSON [2]

(WITH 2 FIGURES)

In 1932 a small amount of an unfamiliar leaf spot on Winter Turf oats (*Avena sativa* L.) was found by the senior writer in the Alsea River Valley, Oregon. In February 1934, the disease was found again and more abundantly on the same host on High Prairie, near Lyle, Klickitat County, Washington (**5**). The attacked plants were somewhat dwarfed, and an abundance of reddish brown spots of various sizes and shapes occurred on the leaves. In addition, the plants also showed considerable reddening aside from the leaf spots. A more detailed description of the development of the disease has been given elsewhere (**6**). Numerous conidia were found on the lesions and these spores were used in isolating the fungus on potato-dextrose agar. The spores germinated readily at 4° C. and invariably produced very scanty growth. At the end of 6 weeks the colonies were barely visible to the unaided eye. At a magnification of 100 times, the colonies could be seen to consist of hyaline hyphae, which clung closely to the surface of the agar. At intervals on the hyphae, a profusion of conidia were borne in fan-shaped whorls, usually laterally or less commonly at the end of short branches. All transfers from these colonies failed to grow.

On examining cross sections of the spore-bearing lesions, it was found that the spores were produced on very short conidiophores compacted together on a poorly developed stroma in the epidermis (FIG. 1). There was no apparent rupture of the leaf epidermis as in typical acervuli. The fungus was considered as

[1] Coöperative investigations by the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the Oregon and Washington Agricultural Experiment Stations.

[2] Assistant pathologist and principal pathologist, respectively, Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

belonging to the Melanconiales and to the genus *Pseudodiscosia* Hösterman and Laubert.

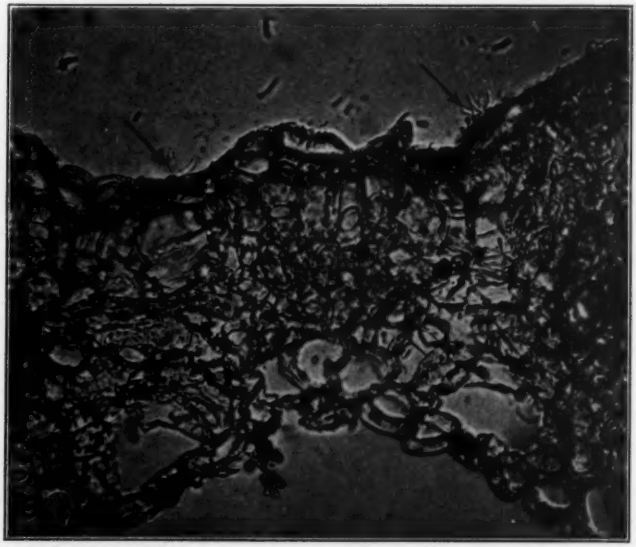


FIG. 1. Cross section of a leaf of *Avena sativa* through a lesion caused by *Pseudodiscosia Avenae*. The fungus occurred throughout the interior of the leaf but was most abundant near the upper surface. Location of the conidiophores and developing spores are indicated by arrows. The section was made by aid of a freezing microtome. × 145.

The type species of *Pseudodiscosia* is *P. Dianthi* Hösterman and Laubert, which causes an important leaf rot of carnation in Europe (**3**). Salmon and Ware (**4**) accepted the name given by Hösterman and Laubert, but Buddin and Wakefield (**1**), after finding that the fungus had a pycnidial form, transferred the species to the genus *Heteropatella* Fuckel.

The fungus on oats differs from *Heteropatella Dianthi* in that the acervuli are less distinct and the conidia are narrower. The length of the conidia, their septation, general form, and the way they are borne on the conidiophores are very similar in the two fungi. Therefore, while they are clearly distinct from each other, apparently they are closely related.

In 1929, Gizhitskaĭa (2) described *Heteropatella graminis* on dry grass stems in Russia. The original description of this fungus is quoted in full as follows:

"Pseudopycnidiis superficialibus, fragilibus, 250–300 μ, diam., atris; conidiis hyalinis, 50–60/4–4, 5 μ, elongato-cylindraceis, apice rotundatis, 10–12-septatis, in setam 50–62, 5/1, 5–2 μ elongatis.

"Ad culmum siccum graminis. Kiovia. In Horto Botanico. 16. X. 1928."

The fungus on oats differs from *Heteropatella graminis* in that the acervuli of the former fungus are less distinct and the spores have fewer septae and are somewhat narrower and considerably shorter than those of the latter fungus.

Thus the fungus on oats differs from both *Heteropatella Dianthi* and *H. graminis* and therefore is here described as a new species. As no pycnidial stage has been found for the fungus on oats, it logically belongs in the genus *Pseudodiscosia*.

Pseudodiscosia Avenae sp. nov.

Mycelium branched, septate, hyaline to faintly tinged with yellow, intracellular or intercellular in the leaf, aggregating at or near the surface, more frequently the upper surface, producing blunt or rarely sharp-pointed 1 to 3-celled (mostly 1-celled) conidiophores 5 to 12 by 0.8 to 2 μ. Conidia with one cilium at each end. Body of spore narrowly fusiform, slightly curved, hyaline or faintly tinged with yellow, 2 to 3 septate, 10 to 42 × 2 to 4 μ (FIG. 2). Conidia are borne singly or sometimes in pairs, acrogenously or subacrogenously. Bases of spores are rounded or blunt with a rod-shaped or sometimes sharp-pointed appendage or cilium, 1 to 16 × 0.3 to 1.3 μ, attached obliquely near the hilum. The apical appendage or cilium usually is longer than the one at the base and usually merges very gradually with the body of the spore.

Mycelium ramosum, septatum, hyalinum vel dilute flavidulum; conidiophora in stromate basilare nascentia, obtusa vel acuta, non septata vel 1–2-septata, 5–12 × 0.8–2 μ; conidia utrinque appendiculata, fusiformia, hyalina vel dilute flavidula, 2–3-septata, 10–42 × 2–4 μ, singulatim vel interdum binatim acrogena vel subacrogena, basi rotundata vel obtusa; appendicula basilaris, oblique prope hilum affixa, 1–16 × 0.3–1.3 μ, appendicula apicalis plerumque longioris.

On leaves of fall-sown oats (*Avena sativa*) in the Alsea Valley,

Lincoln County, Oreg., February 1932, and High Prairie, Klickitat County, Wash., February 1934, forming fawn to dark brown lesions, which are sometimes more or less diffuse and sometimes with red borders. Frequently only the distal halves of the leaves are affected. The affected portions are rather leathery. Attacked plants were somewhat stunted and showed excessive reddening.

FIG. 2. Conidia of *Pseudodiscosia Avenae* drawn with the aid of a camera lucida. × 750.

Co-type specimens have been deposited in the Mycological Collections of the Bureau of Plant Industry, U. S. Department of Agriculture, and the herbaria of the Department of Botany, Oregon State College, Corvallis, Oreg., Department of Plant Pathology, Washington State College, Pullman, Wash., Department of Plant Pathology, University of Idaho, Moscow, Idaho, Department of Botany, University of Wisconsin, Madison, Wis., and The Herbarium, Kew, England.

The writers are indebted to Miss Edith K. Cash, assistant pathologist, Division of Mycology and Disease Survey, Bureau of Plant Industry, U. S. Department of Agriculture. for assistance in preparing the Latin description.

LITERATURE CITED

1. **Buddin, W. & Wakefield, E. M.** The fungus causing the leaf rot of the carnation. Brit. Myc. Soc. Trans. **14**: 215–221. 1929.

2. **Gizhitskaia, Z. K.** Novitates pro flora mycologica. Materials for mycology and phytopathology **8**: 102. 1929.
3. **Hösterman, G. & Laubert, R.** Eine Bösartige neue Pilzkrankheiten der Nelke. Gartenwelt **25**: 65–67. 1921.
4. **Salmon, E. S. & Ware, W. H.** Leaf rot of the carnation. A new and dangerous disease. Gard. Chron. **81**: 196–197. 1927.
5. **Sprague, R.** Observations on diseases of Gramineae in Oregon and adjacent parts of Washington during the open winter of 1933–34. U. S. Dept. Agr. Bur. Plant Indus. Plant Disease Rep. **18**: 24. 1934. [Mimeographed.]
6. ——. A new leaf spot of oats. Northwest Sci. **9**: 15. 1935.

PHOTOGRAPHS AND DESCRIPTIONS OF CUP FUNGI—XXIII. STAMNARIA

FRED J. SEAVER

(WITH 1 FIGURE)

In August, 1934, Dr. J. J. Davis of Wisconsin sent the writer specimens of a fungus on *Thuja occidentalis*, which was not recognized by him. Neither was it known to the writer, and since no fungus had been reported on this host, which seemed to fit, it was decided to publish it as new.

The generic limits of the cup-fungi are not very well defined. After considerable study it has been concluded that this is a *Stamnaria* resembling very closely *Stamnaria Equiseti*. The apothecia occur in erumpent, congested clusters and are extremely gelatinous, shrinking to almost nothing in dried material. A description follows:

Stamnaria Thujae sp. nov.

Apothecia occurring singly or more often in congested masses erumpent through the epidermis on the under side of the foliage of the host, translucent with a slight yellowish or pinkish tin exceedingly soft and gelatinous, shrinking much in drying, the individual apothecia small, not usually exceeding .2 mm. in diameter; asci clavate, reaching a length of 55 μ and a diameter of 15 μ, 8-spored; spores irregularly disposed in the ascus, ellipsoid hyaline, granular 6–7 $\times$ 10–12 μ; paraphyses very slender branched.

Apotheciis gregariis, erumpentibus, hypophyllis, tremelloideis, hyalinis vel subroseis, .2 mm. diam.; ascis clavatis, octosporis 15 $\times$ 55 μ; sporidiis ellipsoideis, granulosis, hyalinis, 6–7 $\times$ 10–12 μ; paraphysis filiformis, ramosis.

On foliage of *Thuja occidentalis*.

TYPE LOCALITY: Baileys Harbor, Wisconsin.

DISTRIBUTION: Known only from the type locality.

THE NEW YORK BOTANICAL GARDEN,
BRONX, NEW YORK CITY

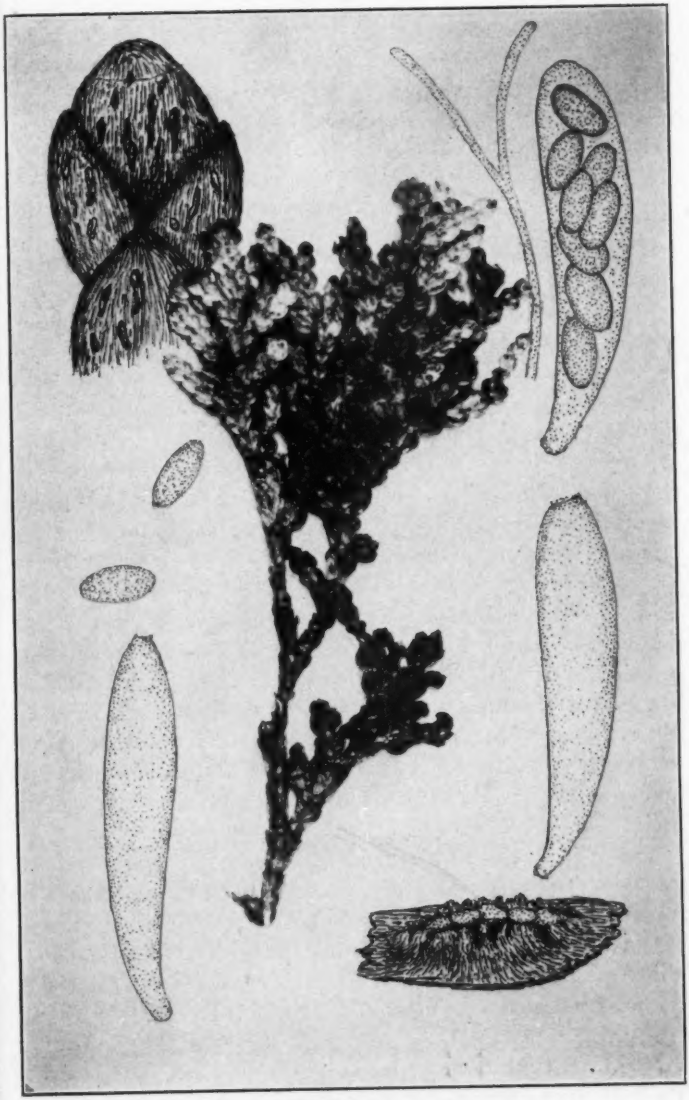


FIG. 1. *Stamnaria Thujae* Seaver.

THE MORPHOLOGY AND DEVELOPMENT OF CALICIOPSIS PINEA

HELENE WALLACE MCCORMACK[1]

(WITH 21 FIGURES)

The genus *Caliciopsis* Peck (**9**) was described by its author as a member of the Discomycetes. Rehm (**10**), Arnaud (**1, 2**), and other students of the taxonomy of the Ascomycetes have agreed with Peck, and in general have placed the genus near *Calicium* of the Caliciaceae. Ellis (**4, 5**) regarded *Caliciopsis* as essentially identical with his own pyrenomycetous genus *Hypsotheca*, but in deference to Peck's opinion did not merge the two. Fitzpatrick (**6**) included the species of *Hypsotheca* in *Caliciopsis*, incorporated the genus in the Coryneliaceae, and expressed the opinion that the family is pyrenomycetous and most closely allied to the Perisporiaceae. Influenced by the work of Miller (**7**), he has since come to regard the fruit-body in *Caliciopsis* as not a true perithecium, but as more of the nature of a loculate stroma such as exists in the Dothideales and allied orders. As no one of these divergent points of view has been based on a cytological and ontogenetic study, it has seemed desirable that one be made. In the investigation here reported, emphasis has been placed on the determination of the method of origin of the ascigerous cavity and ostiolar opening, and on a study of the initiation and development of the layer of asci.

The type species of the genus *Caliciopsis*, *C. pinea* Peck, is found on the trunks and branches of *Pinus Strobus* and has been reported also on other coniferous hosts. It is not uncommon throughout the northeastern United States, and occurs abundantly in central New York. The material used in this investigation was collected at Ringwood Wild Life Preserve near Ithaca,

[1] The writer gratefully acknowledges the assistance and suggestions of Doctor H. M. Fitzpatrick under whose direction this work was undertaken and prosecuted. A summary of the investigation was presented by him at the winter meeting of the Mycological Society of America at Pittsburgh, Pa. in December, 1934.

New York, in the latter part of April 1934. Ascigerous fruit-bodies in all stages of development were found on the bark of *Pinus Strobus* in the typical, smooth, depressed cankers mentioned by Fitzpatrick (**6**: 226) and Overholts (**8**: 235) as characteristic of the disease apparently caused by this fungus. In addition the less conspicuous bodies referred to tentatively by Fitzpatrick as pycnidia were collected. Our studies indicate that they are instead spermagonia.

PREPARATION OF MATERIALS

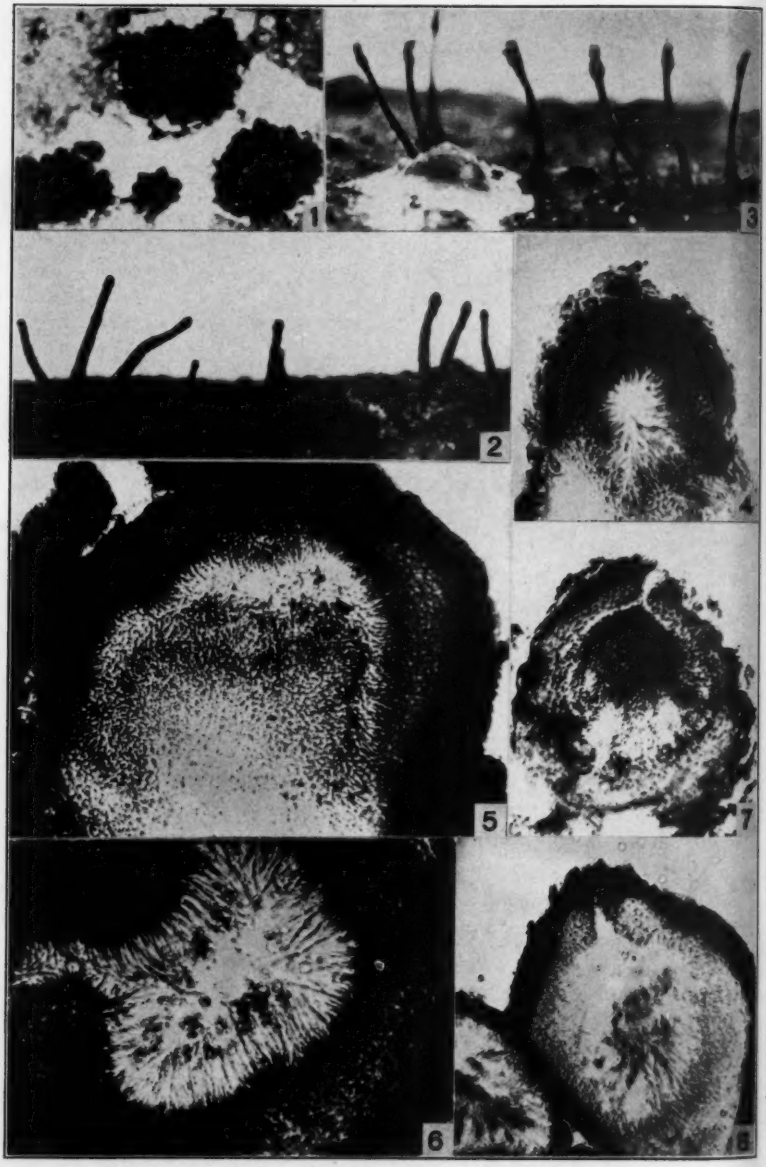
The best preparations of the spermagonia obtained were made by free hand sectioning of the diseased bark. The sections were stained by warming them gently in lacto-phenol and methyl blue. The excess stain was then removed and mounts were made in 50 per cent glycerine.

Ascocarps of various ages, after being removed from the bark and softened by soaking in warm water for several hours, were placed in chrome-acetic acid fixer for twenty-four hours. The material, after washing, was carried into paraffin through butyl alcohol and studied in serial sections 6 to 10 μ in thickness. In staining the material a modification of Heidenhain's iron alum haematoxylin method was used, in which a 1 per cent solution of picric acid is substituted for iron alum in differentiation.

MATURE STRUCTURES

The mycelium of *C. pinea*, as it exists in the cortical tissue of the host, is composed of long, narrow, cylindrical cells. Small, more or less circular, often confluent stromata are formed beneath the outer layer of the bark by the aggregation of the mycelial elements. In early stages these stromata give little external evidence of their presence, but continued growth of the hyphal mass finally causes the rupture of the bark. The small, cushion-shaped stroma, thus exposed, soon takes on a lobed appearance, and in time the lobes develop into spermagonia and ascocarps.

The spermagonium is small, black, and pycnidium-like (FIG. 1). At maturity it measures 100–150 μ in diameter and comes to be filled with rod-shaped to allantoid hyaline or slightly yellowish, single-celled spermatia measuring 2.5–3.5 μ and produced on



FIGS. 1–8. *Caliciopsis pinea* Peck on bark of *Pinus Strobus*.

bottle-shaped or conical spermatiophores A small but definite ostiolar opening is present.

The mature ascocarp (FIG. 3), which appears to the unaided eye as a small black spine, is a stromatic column with an apical or sub-apical enlargement containing a single ascigerous locule. Spermagonia are often found clustered about the base of the column. The surface of the ascocarp is dull to shiny. In texture it is coriacious, becoming more or less gelatinous when moist. The elongated stroma measures 1.75–2.5 mm. in length, is cylindrical, straight or somewhat curved, often swollen at the base and occasionally branched, producing in such cases two or more apical ascigerous swellings.

The asci (FIG. 21) are ovate, 12–19 × 5–8 μ, with long slender stalks, and contain eight small, ellipsoidal to nearly globose, golden-brown ascospores. The spores are freed by the deliquescence of the ascus wall and are pushed out through the opening, giving the tip of the stromatic column a distinctly reddish-brown, fuzzy appearance.

DEVELOPMENT OF THE SPERMAGONIUM

Formation of the cavity of the spermagonium is initiated at the center or toward the apex of a short stromatal lobe by disintegration of the hyphae of that region (FIG. 4, 5). The cavity, thus formed, continues to enlarge through progressive disintegration of the hyphae of the lobe until much of its central tissue disappears. Long thread-like, vacuolated hyphae (FIG. 6) persist for a period in the cavity, but organization of a definite hymenium soon takes place, and finally the cavity is filled with spermatia (FIG. 7) which escape to the outside through a definite ostiolar opening (FIG. 8). Before the cavity is fully formed rather large unicellular, bottle-shaped to conical spermatiophores appear at its border and cut off small rod-shaped to allantoid spermatia. They are slightly smaller than those later developed in the cavity from spermatiophores of essentially the same type.

Similar cases of spermagonia in which two sorts of spermatia are produced have been reported by Dodge (**3**: 747). In both *Guignardia Bidwellii* and *Phyllostictinia carpogena*, according to him, two types of spermatia occur, but those of the first kind

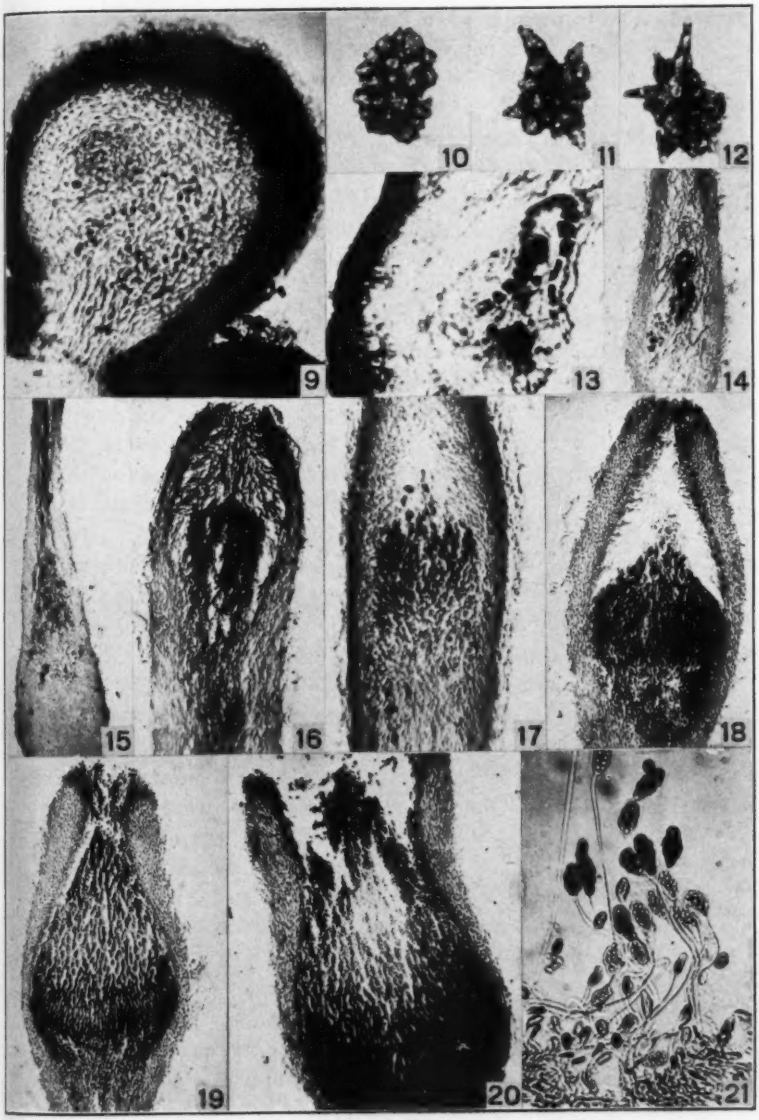
formed are not borne on definite spermatiophores. Instead they result from the disjunction of the cells of thread-like hyphae which fill the cavity in its early stages. Later, as in the case of *C. pinea*, when definite spermatiophores have come to be present, the cavity is devoid of these thread-like aggregations. The reason for the existence of the two types of cells is not clear. In *C. pinea*, several unsuccessful attempts were made to germinate them. This failure of germination has led us to regard both of them as spermatia.

DEVELOPMENT OF THE ASCOCARP

In their early stages the spermagonium and ascocarp, developing together from neighboring lobes of the cushion-shaped stroma, are superficially indistinguishable (FIG. 10). However, in section the two are seen to be different. The lobe (FIG. 9) which is destined to develop into an ascigerous stromatic column reveals in section no cavity, but instead homogeneous tissue in which lie deeply staining hyphae of the nature of archicarps.

The lobe of the stroma in which these archicarps occur (FIG. 13) soon begins to elongate and assumes a conical form (FIG. 11, 12). At this stage its hyphae are long, narrow, and branching and form a more compact peripheral layer enclosing a central core of looser tissue in which the archicarps lie (FIG. 14). As the lobe elongates into a sharp-pointed spine (FIG. 2) the hyphae in its base take on a vacuolate aspect and the walls of adjacent hyphae tend to coalesce (FIG. 15) giving a homogeneous appearance. Meanwhile the cells of the archicarps lose their contents and become less evident. A long bundle of ascogenous hyphae constitutes a core in the center of the rapidly elongating apical portion of the spine. Although the point of origin of these ascogenous hyphae was not traced definitely to the cells of the archicarp such a connection was clearly indicated by the sequence of events.

As the apical region of the column begins to swell, and differentiation of the ascigerous locule is initiated, a profuse branching of the ends of the ascogenous hyphae occurs (FIG. 16). Beyond their tips the hyphae composing the interior of the stroma loosen up and disintegrate to form a definite cavity (FIG. 17, 18) above the developing young asci. Meanwhile, the hyphae composing the outer layers of the stroma become more compact, and their



Figs. 9–21. *Caliciopsis pinea* Peck on bark of *Pinus Strobus*.

walls tend to coalesce as do those at the base of the column in earlier stages. The continuation of lysigenous action at the tip of the stroma results in the formation of the definite opening (FIG. 18) through which the ascospores later escape (FIG. 19).

It will be noted that several archicarps arise in a single ascocarp and present the appearance of a gnarl of large-celled deeply staining hyphae in contrast to the lighter staining hyphae surrounding them. Each archicarp appears to be formed by the transformation of a single multicellular hypha, the cells of which become dense with protoplasm and increase in diameter until they are much broader than the stromatic cells. As the stromatal lobe elongates the archicarp becomes a looser coil, but the number of cells composing it is not easily determined on account of the irregularity and twisting of the several interwoven archicarps.

At the maturity of the archicarp the central cells, having continued to increase in diameter are three to four times the width of the smaller cells and from ten to twelve times that of the stromatic hyphae.

In one section only, a multicellular hypha was seen originating directly from an archicarp, penetrating the tissue of the ascocarp, and reaching the outside. Whether or not hyphae such as this constitute a trichogyne-like apparatus through which fertilization takes place cannot be asserted with certainty. The material was found to be not well suited for cytological investigation, the nuclei being very minute.

At the time that the asci are taking origin from the tips of the ascogenous hyphae (FIG. 17) and are pushing upward to fill the locule (FIG. 18, 19), it becomes evident that the fungus is not discomycetous in type. Paraphyses are absent and there is no palisade arrangement of asci to form a definite hymenium. Instead the asci are seen to compose a broad fascicle in which the individuals stand at every possible height. The ascus is borne on an extremely delicate stalk (FIG. 21) and these stalks in some cases are sufficient in length to extend from the base of the locule to its apex. In longitudinal section the base of the locule sometimes has the aspect of being lined with a palisade layer of young asci (FIG. 19, 20). This is, however, an illusion resulting from superficial observation, the band in the lower part of the locule being in

fact composed of the delicate stalks of asci, whose spore-bearing sacs are to be found throughout the entire interior of the locule. The fasciculate arrangement of the asci, clearly pyrenomycetous in type, is well revealed at higher magnification in figure 21. The ascospores are finally freed from the ascus by deliquescence of the ascus wall and lie free in the uppermost region of the locule. The entire mass of spores tends to cling together, and is pushed upward by the pressure of the developing asci below. Finally the pore which was formed by lysigenous action at the apex of the locule is greatly enlarged as the accumulation of spores bursts through and protrudes beyond the tip of the column as a fuzzy brown plug (FIG. 3). The nearly wide-open aspect which results provides the fungus with its single evidently discomycetous character, and has led Arnaud (**1, 2**) to place *Caliciopsis* near *Calicium*. A consideration of our own observations, here presented, would seem to indicate that the genus falls instead near the Coryneliaceae, as suggested earlier by Fitzpatrick (**6**). In any case it is clearly a stromatic genus in which the ascigerous cavity is a locule.

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LITERATURE CITED

1. **Arnaud, G.** Contribution a l'étude des Fumagines,—III. Ann. Ecole Nat. Agric. Montpellier, n.s. **12**: 23–54. *13 fig.* 1912–13.
2. ——. Les Asterinees—V. Ann. des Epiphyties: 235–275. *pl. 1–9, fig. 1–11.* 1930.
3. **Dodge, B. O.** Origin of the central and ostiolar cavities in pycnidia of certain fungous parasites of fruits. Jour. Agr. Res. **23**: 743–759. *pl. 1–6.* 1923.
4. **Ellis, J. B. & Everhart, B. M.** A new genus of Pyrenomycetes. Jour. Myc. **1**: 128–129. 1885.
5. ——. Hypsothèca Ell. & Ever. North American Pyrenomycetes: 199–200. *pl. 22, figs. 1–5.* 1892.
6. **Fitzpatrick, H. M.** Monograph of the Coryneliaceae. Mycologia **12**: 206–267. *pl. 12–18, tab. 1.* 1920.
7. **Miller, J. H.** Biologic studies in the Sphaeriales—I. Mycologia **20**: 187–213. *pl. 21–22, fig. 1–3.* 1928.
8. **Overholts, L. O.** Mycological notes for 1928–29. Mycologia **22**: 235. 1930.
9. **Peck, Charles,** Report of the Botanist. Ann. Rep. N. Y. State Mus. Nat. Hist. **33**: 32. *pl. 2, fig. 11–15.* 1880.
10. **Rehm, H.** Calicieae, *in* Rab. Krypt. Fl. **3**: 382–414. *30 figs.* 1896.

EXPLANATION OF FIGURES

Caliciopsis pinea Peck on bark of *Pinus Strobus*

Photographs by W. R. Fisher. Fig. 1, caespitose clusters of spermagonia, × 10; 2, spine-like stromatic columns, some of them beginning to form the apical enlargement in which the ascigerous locule lies, × 10; 3, mature ascocarps, the apices fuzzy from the extruded mass of ascospores and asci; spermagonia visible at the base, × 14; 4, longitudinal section of a stromatic lobe which has begun to develop into a spermagonium; the central cells disorganizing to form the spermagonial cavity, × 380; 5, longitudinal section of a similar lobe in which the hymenium of spermatiophores has been initiated, × 380; 6, section of a young spermagonium showing vacuolated hyphae lining the enlarging cavity; spermatium-like cells of the first type present, × 380; 7, section of a mature spermagonium almost completely filled with spermatia, the vacuolated hyphae having disappeared from the cavity, × 380; 8, longitudinal section of a spermagonium showing the ostiolar opening at the apex, × 380; 9, rather thick, free-hand, longitudinal section of a stromatic lobe which has begun to develop into an ascocarp; in its interior the deep-staining elements of developing archicarps evident and cavity formation lacking, × 380; 10, 11, 12, early stages in ascocarp formation, the hemisphaerical stromatic lobes beginning to elongate and assume the aspect of spines, × 25; 13, a group of archicarps surrounded by the tissue of the stromatic lobe, × 380; 14, archicarps evident at the center of a young elongating stromatic spine, × 75; 15, a bundle of ascogenous hyphae arising from the region of the stroma occupied by the archicarps and constituting a core in the elongating spine, × 75; 16, longitudinal section of the apex of the stromatic column showing the much branched tips of the ascogenous hyphae forming a deep-staining mass in the basal portion of the developing locule, × 215; 17, a somewhat later stage in which ascus-formation has begun, and lysigenous action has broken down the stromatic elements to give a locule, × 215; 18, the locule definitely outlined in the enlarged apex of the stromatic column, and the broad fascicle of developing asci filling its base, × 215; 19, the locule filled with asci, and provided apically with a definite pseudo-ostiolum formed by disintegration of the stroma at that point, × 215; 20, the pressure of asci and ascospores from below resulting in the enlargement of the ostiolar opening and the extrusion of the ascospores as a mass which has been in part washed away in the process of the preparation of the slide, × 260; 21, a group of asci removed from the ascocarp and photographed to show the fasciculate arrangement and the long delicate stalks, × 380.

NOTES AND BRIEF ARTICLES

THE MYCOLOGICAL SOCIETY OF AMERICA

Report of the Fourth Annual Meeting

The fourth annual meeting of the Mycological Society of America was held December 31, January 1, at St. Louis, Missouri, in conjunction with that of the American Association for the Advancement of Science. The Society was represented on the Association Council by Fred J. Seaver and Carroll W. Dodge. The headquarters of the Society were at the Hotel Statler. This hotel served also as headquarters for the Botanical Society of America, American Phytopathological Society, and other botanical groups. The sessions of the botanical societies were held at Washington University. Registration was at the Municipal Auditorium. Arrangements for the Mycological Society were made by the local representative, Carroll W. Dodge.

The retiring president, Bernard O. Dodge presided at the sessions and gave as his address a paper entitled "Facultative and Obligate Heterothallism in Ascomycetes." As retiring vice-president of Section G. of the A. A. A. S. he gave a paper on "Reproduction and Inheritance in Ascomycetes." The Society held the usual joint sessions with Section G and the American Phytopathological Society. At the regular sessions a smaller number of papers than usual were presented, but some were of outstanding interest.

At the business session the election of new officers for 1936 was announced as follows: Harry M. Fitzpatrick, president, A. H. Reginald Buller, vice-president, David H. Linder, secretary-treasurer, Bernard O. Dodge, councilor. The council named Frederick A. Wolf to serve an additional five-year term as associate editor of MYCOLOGIA. The roll of the Society for 1936 now includes approximately 350 names, and the membership is slowly growing.—H. M. FITZPATRICK, *Secretary-Treasurer*

Atractobasidium Grandinia (Rick) comb. nov.

Through the kindness of Dr. Gladys E. Baker of the Henry Shaw School of Botany, my attention has been called to the description of *Platygloea grandinia* Rick, Egatea 18: 211. 1933, and I have been permitted to examine an authentic specimen, determined by Rick, in the collection of the Missouri Botanical Garden. It proves to be identical with the species described as *Atractobasidium corticioides* Martin, Bull. Torrey Club **62**: 340. 1934. As stated in the latter reference, the fungus is not a *Platygloea*, but since Rick's specific epithet has precedence it is necessary to propose the new combination *Atractobasidium Grandinia* (Rick).—G. W. MARTIN.

KEY TO THE BOLETACEAE

The Rhode Island Botanical Club has published a pamphlet entitled "Tentative Keys to the Boletaceae of the United States and Canada," by Walter H. Snell. As suggested by the title, these keys are not a final product, but, as the result of several years of study, represent the progress made to date in eliminating much of the confusion that has prevailed in this family in this country. It is believed that these keys will enable collectors of the higher fungi to identify with some degree of certainty the boletes they find, instead of ignoring them or putting them away without notes and unnamed even tentatively, as apparently has too commonly been the case in recent years.

In addition to the keys, this treatment contains four pages of "Aids to Rapid Identification," by the use of which difficult or ambiguous choices in the keys may occasionally be clarified, or identifications reached in short order by the narrowing of possibilities. For example, three of the headings in this section are—"Pileus with no red," "Flesh peppery to taste" (one species), "Spores under 8 μ long" (5 species named).

This publication is available for free distribution in single copies to individuals and institutions. To institutions desiring more than one copy, the price is 50 cents a copy. Address the author at Brown University, Providence, R. I.

BRITISH STEM- AND LEAF-FUNGI

This volume by W. B. Grove is devoted to the Sphaeropsidales to the end of the Sphaerioideae which have colorless or nearly colorless spores. The Fungi Imperfecti, or Deuteromycetes, are divided into two large groups: (1) those which bear their spores within some cavity of the matrix on which they grow, to which the author of this book gives the name Coelomycetes; and (2) those which bear their spores outside the matrix, which have long been known as Hyphomycetes.

It is the colorless spored forms which Grove is considering in the present volume. In the larger genera, such as *Phyllosticta*, the species are arranged on the basis of host characters in alphabetical order. Each species is accompanied by a brief description of the diagnostic characters. These are accompanied by notes on its relationship, or possible relationship, to other species. The imperfect fungus is included even though the perfect is known. Also suspected connection with a perfect stage is noted.

A number of new species are described, with Latin diagnoses in the back of the volume. A few text figures accompany the descriptions. The volume (i–xx + 1–488) is printed in the United States and may be secured through the Macmillan Company, New York, for seven dollars ($7.00).—F. J. SEAVER.